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THE
AMERICAN NATURALIST

VOL. LXVII *November–December, 1933* No. 713

THE GENETICS SOCIETY OF AMERICA

THE PROGENY TEST AS A MEANS OF EVALUATING THE BREEDING POTENTIALITIES OF FARM ANIMALS

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THE service which genetics may render to agriculture through improvement in the value of farm animals as a source of income to the farmer is of real importance, because it contains the possibility of introducing into agriculture an efficiency in farm operations which will raise the income labor receives on the farm to a par with that of labor in industry. If genetics can successfully perform this service, it will also render a service to itself by broadening the field of its activities and potentialities. To understand how this may be accomplished, it is necessary first to have a clear comprehension of what is required of genetics in this field.

The application of genetics to the improvement of plants and animals of agricultural importance, takes genetics into the field of business, because for the most part agriculture is engaged in producing commodities for the general market which must therefore return a margin of profit to the producer, for without profits no business long survives. Genetics, therefore, if it is to be of service to agriculture, must in some way be able to produce business profits, otherwise agriculture will have no place for it.

[1] Contributed to a symposium on "The Progeny Test as a Means of Evaluating the Breeding Potentialities of the Individual," held by the Genetics Society of America at Atlantic City, N. J., December 27, 1932.

Profits arise in business when the selling price exceeds all costs of production. Since the farmer both buys and sells in a market where prices are fixed by influences beyond his control, he is compelled to seek his profits in the narrow field between costs and selling price; that is, in those operations on the farm over which he exercises some measure of control.

As the great crops of the farm, such as hay, corn, etc., are not produced for human consumption but are mostly fed to farm animals to produce other products better suited to man's needs or desires, the efficiency of farm animals in converting these crops into salable products becomes of great importance. Genetics, then, must introduce greater efficiency into the operations of animal husbandry on the farm, by producing animals of greater productive capacity or greater ability in the conversion of the bulky crops of the farm into products consumed as food by man or otherwise directly serving human needs than those now available.

Thus the improvement of farm animals is a matter of improvement in those qualities which contribute to the livelihood of the farmer, either in his home or through sale in the markets of the country. The progeny test, therefore, must be considered from this standpoint.

Improvement of farm animals—in the minds of many people—deals with wholly non-commercial subjects, such as improvement in type, color and other features which dominate the show ring. In saying that such features are non-commercial, the fact that some people derive an income from operations in characters of this kind has not been overlooked, but the value of the articles they sell depends upon the whim of individuals and will not be found quoted in the daily papers as will the price of butter or wool. They are, therefore, of no real commercial value. Moreover, the world of commerce will not pay a penny more for the products which come from champion show ring animals than from those less famed in this respect. All it cares about is the quality of the goods it buys and sells. For this market, those animals which

most cheaply produce the goods it requires are those most suited for general farming. I shall therefore deal with the progeny test as utilized in the improvement of farm animals solely from the standpoint of commercial usefulness.

At once a question arises in connection with the meaning of improvement. Does it refer to occasional individuals or averages? Clearly averages, because while improved individuals are important as stepping-stones to improved averages, it is only when the average of the race is improved that the improvement comes to have commercial significance. When a dairy cow makes a world's record, it marks no improvement in average dairy cows. Improvement in dairy cattle acquires commercial significance only when the average yield of dairy cattle is increased. The use of the progeny test in the improvement of farm animals has meaning then, only as improvement in averages is brought about.

Having stated these general conditions relating to the progeny test in the improvement of farm animals, we are in a position to consider the test itself. Though often considered to be of comparatively recent origin, perhaps because it is the foundation of the very modern science of genetics, breeders have attached considerable significance to the progeny test for a long time. The word prepotent—used by breeders long before genetics came into being—is indicative of the recognition given progeny as a guide to the breeding value of the individual, but they did not know how to utilize the progeny test, for the true nature of inheritance was still a mystery. It required the genius of Gregor Mendel, by bringing order out of seeming chaos, to make the progeny test the foundation upon which a real science of inheritance could be built. The development of this science thus far has been along the lines of acquiring a knowledge of the processes of inheritance, but, as the program of the Sixth International Congress of Genetics held last summer reveals, very little consideration has as yet been given to the utilization of the knowledge thus gained in the improvement of the

plants and animals on our farms. Here is a great undeveloped field of human endeavor the potentialities of which are fully as great as those in the fields of chemical or electrical engineering.

In the application of genetics to the improvement of agricultural plants and animals, the principles upon which it is established are the best guide in all practical breeding operations. There are, however, numerous modifications of detail which are imposed by differences in the plants and animals concerned, but their number is so great that it is impossible to do more than outline some of the possibilities.

The essence of the progeny test, briefly stated, consists in determining the number and proportion of the various kinds of progeny produced by an individual and from these to derive a statement of its breeding ability. This statement, when reduced to a formula, constitutes the genotype of the individual. However, in the case of all farm animals—unlike many plants—an individual can not reproduce by itself alone but requires the aid of a member of the opposite sex. Always the progeny of farm animals is the result of the joint contribution of two individuals, and so the progeny test must take this fact into consideration.

The situation is further complicated by the existence of two distinct groups of characters. In the one group, characters can be recognized and studied in each sex; in the second group which includes several of the most important economic characters such as milk production, litter size or egg production, the character appears in one sex alone. This state of affairs not only halves the number of progeny available for determination of the parental genotypes but renders impossible the use of the appearance or performance of the individuals of one sex as a guide to their own possible genotypes. Selection in this sex, therefore, is essentially a random process although the field of selection may be narrowed by means of sibs' appearance or performance.

Two other factors, which complicate the use of the progeny test, are of sufficient importance for mention here. One is number of progeny, the other, length of reproductive life. As regards the first, in some instances the number of offspring produced by an individual is so small as to be insufficient for satisfactory application of the progeny test. This is a serious limiting factor in the case of female sheep, horses and cattle, where the number of offspring produced during the life-time of each female is too small to provide a satisfactory random sample of her potentialities.

Length of reproductive life is another limiting factor of importance because by the time the individual has been tested and its breeding potentialities known, it is no longer capable of producing offspring. This factor will probably be found of decisive importance in deciding how to use the progeny test when dealing with such a character as rate of growth in hogs where there are difficulties in obtaining further offspring from females whose breeding potentialities have been determined.

Besides these difficulties in handling the progeny test, there is another which makes necessary further changes in applying it to farm animals. Several characters of the greatest economic importance are quantitative, each being a single expression for the activities of many genes. Present genetic technology does not permit us to analyze these characters by determining the number of genes and mode of inheritance of each, the effect of linkages and so on. We are obliged to deal with the genes in the mass as expressed in a single numerical value.

In contrast, then, with the material with which genetics ordinarily concerns itself, which is relatively simple and easy to handle, many of the most important characters, with which those who would apply genetics in the improvement of farm animals must deal, are exactly those things with which genetics finds great difficulty. Moreover, one of the tools which genetics commonly employs, crossing of races followed by inbreeding, do not yield results comparable with those obtained in the case of sim-

pler material. For one reason, domestic races of animals are not genetically pure. For a second reason, popular prejudice against so-called "racial" crosses is very great. Also, where inbreeding followed by crossing is the method employed, the expense and time required to inbreed is so great and the results of subsequent crossing so uncertain in value that progress along these lines is very doubtful. So until new methods are developed that permit of more rapid and reliable improvement than any hitherto available, reliance must be placed upon selection as the chief tool to be used in improving farm animals. Selection has as its objective the identification and propagation of those superior individuals which are believed to be capable of reproducing their good qualities in their offspring. Here the progeny test becomes extremely valuable, for by its aid—and I think that no one will question its indispensability—it is possible to obtain a reading of each breeder's worth and thus recognize those individuals which should be continued in active service as well as the best manner of mating them in the future. The progeny of the individuals thus shown most suitable for a given purpose provide a new generation of breeders to be subjected to the same rigorous tests. Moreover, if improvement in racial averages is to be made, a sufficient number of superior individuals must be discovered, and they must not only produce superior offspring on the average but they must produce them in sufficient numbers so that it becomes possible to discard all individuals of inferior breeding ability together with their progeny.

The process of selection must be continued in operation in each succeeding generation if continued improvement is desired. Here the progeny test may be used as a means for selecting in each new generation those individuals which are to be used as breeders, for among the various breeders of the last generation some have produced progeny which are superior to the progeny of others, and are, therefore, the ones from which to select parents of the next generation, which in turn are subject

to classification of breeding ability by the character of their progeny.

While all are agreed upon the indispensable nature of the progeny test, we are still confronted by the various considerations affecting its utilization which have been mentioned earlier in this paper. In some cases it is possible to follow ordinary genetic methods but, generally speaking, the progeny test, when applied to the improvement of the average value of economic characters, must be adapted to the peculiarities and requirements of each case. Improvement in yield or quality of wool may require different treatment than improvement in yield of pork and both will differ from improvement in milk yield, while the development of an all round farm horse, capable of pulling heavy loads at a rapid pace more economically than a tractor, presents still another problem. As space does not permit of a review of all possibilities, it is necessary to confine the discussion to a single instance. For this purpose the dairy cow is an excellent example because in this case the progeny test must be applied to a quantitative character, expressed by the female alone and where, moreover, it can be applied successfully only to the male because each female not only has a small number of offspring but reproduces so slowly that the few offspring obtained give just an inkling of her breeding potentialities which comes so late in her life that her further usefulness as a breeder has already passed before this small view of her breeding abilities is obtained.

Dairy production, whether it be considered as milk yield in its native state or one of its constituents, such as fat yield, is quite clearly a quantitative character resulting from the activities of many genes. No evidence has been produced that it is governed by one or two major genes. Indeed dairy production must necessarily be governed by many genes because the degree of yield is certain to be conditioned by the activities of many parts of the body other than the mammary gland.

Quantitative characters, governed by multiple genes, exhibit in inheritance peculiarities which are not exhib-

ited by the simpler forms of inheritance with which genetics commonly deals. These peculiarities not only affect the utilization of the progeny test but influence racial characteristics. As these peculiarities appear to have received less attention than their importance in dealing with quantitative characters of commercial importance warrants, I propose to consider them very briefly.

(1) The phenotype is a single numerical expression of the activities of the entire group of genes concerned with any particular quantitative character, and is the only objective criterion of their activities either singly or in the mass.

(2) There are marked differences between multiple genes according as the individual genes are non-dominant or dominant. The non-dominant will be considered first because their behavior is so simple and regular.

A. Non-dominant genes.

(a) In the case of non-dominance, a gene in the simplex condition contributes to the phenotype half of its contribution in the duplex condition. That is,—

$$AA = 2 \quad Aa = 1 \text{ and } aa = 0$$

So also for B, C, etc.

(b) As a consequence of (a) the numerical value of the phenotype is identical with that of the genotype, and so—barring of course environmental influences—the numerical value of the breeding potentialities of any individual can be determined without resort to breeding tests, thus giving phenotypic selection of breeders a high degree of effectiveness. Consequently the usefulness of the progeny test is restricted. Space does not permit of further consideration of this point at this time.

(c) The curve of variation, when genes are non-dominant, is always symmetrical unless modified by non-genetic causes.

B. Dominant genes.

Turning now to dominant genes, a much more complicated situation is found.

(a) A gene in the simplex condition makes the same contribution to the phenotype as in the duplex. That is: AA and Aa make the same contribution to the phenotype and are therefore indistinguishable from one another. Also, they differ phenotypically from aa by the same amount. That is:

$$AA \text{ and } Aa = 2 \text{ and } aa = 0$$

(b) As a consequence of (a) the correspondence between genotype and phenotype existing in the case of non-dominant genes is lacking. The rôle of the phenotype as a basis for selection of breeders is less important than in the case of non-dominant genes and the value of the progeny test correspondingly greater.

(c) Many kinds of curves of variation result from dominant genes. Their exact character depends upon the number of genes involved, the relative contribution of each dominant gene, and the ratio of each dominant allelomorph to its recessive in the population at large. Only the briefest mention can be made of these factors and their influence upon the type of curve in relation to the utilization of the progeny test.

Suppose that each different gene contributes exactly the same amount to the phenotype, $A = B = C$, etc. Under these conditions the F_2 ratios differ from those where $A \lesssim B \lesssim C \lesssim D$, etc. Thus, an F_2 ratio with two pairs of genes becomes 9:6:1, instead of 9:3:3:1. Now it is convenient to work with genes of equal numerical value in deriving the theoretical consequences of dominant genes, partly because the problem is simplified but also because this value represents the central value of a series of values and so the broad outline of the curve is

established. In studying, then, the influence of number of pairs of genes upon the curve of variation, it is found that as the number of pairs increases the shape of the curve also changes gradually from a shed-roofed distribution, to a skewed curve of usual form.

The slope of this curve is governed not only by the number of different pairs of allelomorphs, but by the ratio existing in the population between each dominant allelomorph and its respective recessive. Omitting details, as the frequency of the dominant allelomorph of each pair of genes increases, the curve becomes skewed more and more toward the higher values of the phenotypes and variability tends to decrease. If the frequency of the recessive allelomorph increases, the curve of variation becomes symmetrical, flatter and of increased variability.

There is a feature of these curves which is of importance because of its bearing upon the utilization of the progeny test. When the number of genes is not too small, the genotypes corresponding to the phenotypes comprising the curve either possess the average ratio of homozygous dominants to heterozygotes or a ratio not far removed therefrom. Moreover, except when the number of pairs of allelomorphs is very few, or the ratio in the population of each dominant allelomorph to its respective recessive is large, the frequency of these phenotypes—numerically large—as well as those phenotypes that contain few or no dominants—numerically small—is very small, so small in fact that they are very unlikely to occur in random samples of the population. Ordinarily in any sample the ratio of homozygous dominants to heterozygotes will be near or at the average of the population to which they belong.

The bearing of these facts upon the determination of the breeding ability or genotype of the individual arises in this way. The characters, such as milk yield, of which a genotype or its numerical equivalent is desired are variable characters. Variability in the absence of self-

fertilization implies genetic impurity or heterozygosis. We know from the work of Hardy ('08) and others that a population maintains the same distribution of genes—and so the same degree of heterozygosis—generation after generation under conditions of random mating and equal fertility. For purposes of discussion such a population may be considered as an F_2 generation, in that the problem of applying the progeny test contains many of the same elements that one would encounter if he were working with an F_2 population of a kind where each gene could be handled separately. With such a population, one would very likely, as a first step in using the progeny test, proceed to establish a stock of multiple recessives against which to test those individuals whose breeding ability is to be determined, because he knows that the character of the progeny of such test matings will at once reveal the genotype of the individuals under test. This procedure is unquestionably the most direct means of evaluating the breeding potentialities of the individual where conditions permit of its application. Perhaps some day it may be possible to apply it in the improvement of farm animals but at present there are so many difficulties in the way of its adoption that other means must be substituted. A possible alternative is the employment of a group of average individuals against which to test breeders. But here difficulties as related to farm animals are encountered because, as in the case of dairy cattle, groups of average individuals are not as a rule practical, for the testing is done by individual farmers on herds of different levels of productive ability. A satisfactory solution of the problem of determining the breeding potentialities of the individual must take non-genetic as well as genetic factors into consideration in deciding upon the method most suitable for practical use.

Now there is a relationship between the numerical values of the parents' phenotypes and the average of the offspring's which can be utilized very satisfactorily in calculating a rating of breeding potentialities of any one

of the three when the other two are known and which, therefore, is of great practical usefulness in a case like that of the dairy sire, where the character to be improved is expressed in females alone, in that the average of the offspring tends to fall between the parents. In the case of a character wholly controlled by non-dominant genes, the offspring's average always falls exactly half-way between parents. Also, in the case of dominant genes where the ratio of recessive allelomorphs to the dominant is large so that homozygous pairs of dominant allelomorphs are few and far between while heterozygotes and homozygous recessives are numerous, the offspring's average falls at or very near the half-way point.

If, in place of non-dominant genes or dominant genes with a marked excess of recessive allelomorphs, we deal with dominant genes in which there is either equality in number between the dominant and recessive allelomorphs or an excess of dominants, the offspring no longer fall half-way between parents but tend to fall nearer the higher parent, the degree of nearness depending among other things upon the proportion of dominant allelomorphs in the population:—the greater this proportion, the nearer the offspring's average to the higher parent. The exact position of the offspring in any population of this sort will vary according to the genotypes involved in each particular mating, but the frequency distribution of the genotypes centers around an average which can be utilized very satisfactorily in obtaining a rating on the individual breeder. For example, in the case where the frequency of occurrence of each dominant allelomorph to its respective recessive is one to one, giving a phenotypic ratio of 3D to 1R for each pair of allelomorphs, the offspring's average tends to fall two thirds of the way between parents toward the higher one. This happens because throughout that portion of the phenotypic curve containing the bulk of the population, there are on the average twice as many pairs of heterozygous genes as there are homozygous dominants. As in this case only dominant genes are under consideration, a quantitative

difference between two individuals arises only when the number of pairs of homozygous recessive genes in one differs from that in the other and as, on the average, in this example there are twice as many heterozygotes as homozygous dominants in the population, it follows that the average difference is represented by three pairs of recessives in the smaller to one pair of homozygous dominants and two pairs of heterozygous dominants in the larger or some multiple of this ratio. When then two individuals are mated which differ by the average amount, it is clear that the offspring will fall two thirds of the way between parents toward the higher parent, because the mating between the homozygous dominant pair of allelomorphs and the homozygous recessive pair gives offspring which are phenotypically dominants, while the mating of the heterozygous dominants with the homozygous recessives gives offspring half of which are phenotypically dominants and half phenotypically recessives. That is, in this latter case the numerical average of the offspring's phenotypes is half-way between the parental phenotypes while in the former case the offspring's phenotype is exactly like the higher parental phenotype. Since there are twice as many of the former as the latter, the average for both kinds works out at two thirds of the difference of the numerical value of the parental phenotypes. Here is an average value for the offspring's position which can be utilized in determining either parent's phenotype or the offspring's average phenotype when any two of the three are known.

There are two features of this method of arriving at breeding potentialities which require further discussion. One is the fact that the phenotype rather than the genotype is determined. The other the fact that work is done with an average value rather than the particular value which should be known for each particular pairing of genotypes if perfect accuracy in determinating either the phenotype or genotype is to be had. These two matters are somewhat interdependent and so can not be considered entirely apart from one another.

The real question at the moment is whether by use of this method a rating of a parent can be obtained which will result in such improvement in the average of dairy cows that the business of dairying becomes profitable, not whether genetic perfection is obtained. And, as will be shown, the rating given to a parent—based upon the use of the average position of the offspring between parents—is so related to its genotype that it serves practical needs and makes possible the improvement in dairy ability which is so much needed.

The first question relates to the value of the phenotype as a guide to the breeding potentialities of the individual where multiple dominant factors are concerned. This is a numerical expression and for most individuals it bears a definite or near definite relation to the genotype because many individuals are average or near average and have the average ratio of homozygous dominants to heterozygotes, or a close approximation thereto. Of the remainder of the population there is only a small fraction where the departure from the average ratio is sufficiently great to affect the practical significance of the phenotype as a measure of its genotypic value.

As for the use of an average position of the offspring rather than that particular position which results from the particular genotypes concerned in each mating, it happens very fortunately that when the average position of the offspring is used, the calculated rating agrees with the phenotype only when matings are made between individuals in which the average ratio of homozygous dominants to heterozygotes exists. In other cases, the calculated rating is higher than the phenotype when the proportion of homozygous dominants is greater than the average and less when the proportion is less. Thus the calculated rating is parallel to the genotypes and provides a series of values which enables the breeder of farm live stock to distinguish those individuals which should be continued in service from those which should be discarded, and to mate them properly.

There is a graphic method which shows very clearly the way in which offspring fall between their parents (Fig. 1). In this method the females to which a male is

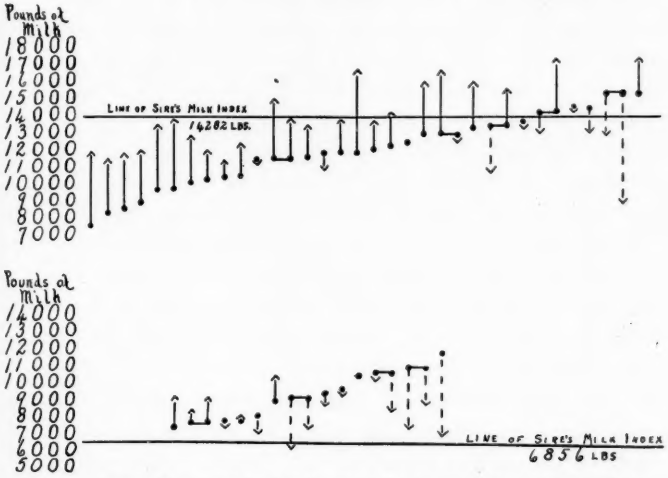

FIG. 1. A graphic method of indicating the transmitting ability of sires. Dots represent dams' character, and arrow head daughters'—in this case amount of milk—plotted against the scale at the right. Two sires are shown of which the one above is evidently superior to the one below. Charts like this can be constructed for quantitative characters in general.

mated are plotted against a scale in ascending order of their phenotypes from left to right and the offspring of each female plotted against the same scale directly above or below their respective dams. The charts of the two males show that there is a level for any particular male, below which his daughters tend to be above their dams and above which they tend to be below. This level, calculated by the method suggested above, evidently represents the individual's breeding potentialities. Of course it is possible—although not as easily accomplished—to construct charts for the female. In the case of the male, charts have been constructed for several characters in three species of animals and found to possess the same general characteristics. These charts possess special advantages for the study of the inheritance of all quantitative characters resting upon a multiple factor basis.

What use is to be made of these facts in dealing with such a case as the improvement of dairy ability, which is expressed phenotypically only in females? The absence of such expression in the males means that a guide for distinguishing dairy ability is totally lacking. Improvement is next to—if not actually—impossible when bulls are selected for breeding at random, which is what selection without a progeny test amounts to. In fact, no improvement in the inherited capacity of dairy cattle has ever been accomplished for it appears probable, from the accounts of dairy production written in the middle ages, that the dairy cattle of that time would respond to modern feed and management as well as present dairy cows. Moreover, in this case progress is hampered by the peculiarities of reproduction in dairy cattle which have been indicated earlier in the paper.

In the case of the bull, however, sufficient progeny can be obtained several years before he becomes useless as a breeder to enable a reading to be made of his potentialities as a breeder. Then the question arises as to the method to be adopted in reading the results of the progeny test. As inheritance in this instance is biparental, it is necessary in some way to determine what the progeny is receiving from their sire and what from their respective dams. If it were possible to mate the bull under test to cows that are completely homozygous for all recessive genes, or some similar uniform test material, the progeny would themselves furnish the required reading but since each of these methods is impossible of application in a practical way, the only method remaining is to take advantage of the fact that in multiple factor inheritance the offspring fall between sire and dams and to use the performance of the bull's daughters in relation to that of their dams in rating his breeding potentialities.

The rating so derived identifies both those sires that should be continued in service and is a guide to the selection of the cows to which they can be mated most advantageously. If the policy of using the right bulls on the right cows is followed continuously for a number of gen-

erations there will be a constant rise in production in the females and in the breeding potentialities of both sexes. If this plan is adopted by a group of breeders, even if the group be small, it will slowly but surely raise the average production of all dairy cattle through the distribution among farmers of the superior genotypes thus developed, especially males, of which there is always a surplus beyond the requirements of any group of breeders.

Having arrived at the conclusion that a rating on the breeding potentialities of the dairy sire can be obtained by taking advantage of the fact that his daughters' average production falls between himself and their dams, what point is to be taken as the position of the daughters to use in the calculations? Fortunately this is a matter of minor practical importance, because any position not too far from the half-way point gives ratings which are not only satisfactory in general but which possess the practical advantage of being stated in terms and amounts that are well suited for use by farmers who carry on the actual breeding operations. However, in view of the attention which has been given to this matter in the agricultural press, certain aspects of theoretical importance may be discussed briefly.

As has been shown above, the average position of the offspring relative to their parents depends upon a number of factors, but in any case there is an average position which by this fact becomes the one most suitable for use. Any other position would lie at one side of the average and would therefore be less representative of actual conditions. Nevertheless, some students of the subject believe that in all cases the offspring should be placed half-way between parents, on the ground presumably that inheritance from sire and dam is approximately equal. This is true, but genotypes are interpretations of relationships between phenotypes and are not themselves determined by observation which can be made only on phenotypes. If, then, the average numerical phenotype of the offspring is treated in every case as though it came at the half-way point, there is a departure from fact be-

cause the offspring's average numerical phenotype does, under certain conditions, fall elsewhere than half-way between parents.

Some have urged that, when the average position of the offspring's phenotype falls above the half-way point (and correspondingly for cases where it falls below), there would be an automatic increase in the quality concerned. This view appears to be based on the age-old confusion between phenotype and genotype; between appearance (or performance) and breeding ability. What really happens is that the average phenotype of the daughters is not only composed of a number of different phenotypes, but these phenotypes represent different genotypes which in turn produce, by segregation and recombination, other genotypes and their respective phenotypes, some of higher and some of lower numerical values. Thus there is a constant interchange of genes according to the rule of Hardy ('08) and so no automatic increase in the quality concerned.

Dairy cattle apparently belong in the class where the offspring's average is nearer the higher parent. Representatives of races of cattle which have different average levels of milk yield have been mated together and the position of the offspring determined. In all the published cases—ten in number—the milk yield of the resulting offspring is reported to be nearer the higher parent. The published figures indicate two thirds or thereabouts as a fair approximation to a value which can not at present be determined more accurately.

But since different races of cattle were used in these interracial matings, does not the average position of the daughters near the higher parent represent nothing more than partial heterosis? To answer this question fully would take us too far afield. All we can say here is that when hybrid vigor was the term favored for what is now called heterosis, it meant that the offspring exceeded both parents in vigor or size or some other quality. There can be no such thing as partial heterosis in the true meaning of the term. The application of the term partial

to heterosis has doubtless arisen because in discussions of the multiple factor theory it is assumed that non-dominance is the rule. In this case the offspring average exactly half-way between parents. Since in experimental crosses involving multiple factors it often happens that departures—some of them wide—from the half-way rule occur, the conclusion has been reached that heterosis is involved in some way. If the consequences of dominant genes in multiple factor inheritance had been considered, it would at once have been apparent that the departure of the offspring from the half-way point was the result of dominance associated with heterozygosis.

The case of dairy cattle illustrates the adaption of genetic principles to a particular case in bringing about improvement in a character of very large economic importance, where ordinary genetic methods are not applicable. Adaptation to circumstances is a fundamental fact of all existence, without which survival is impossible. During the last thirty-odd years a great fund of knowledge of the processes of inheritance has been accumulated by prolonged study and experiment, but only a beginning has been made in its utilization. Full utilization of genetics will be made only when the lead of physics and chemistry is followed in the use of the progeny test for, in a wide sense, the development of physics and chemistry has also been based upon a progeny test. Both have developed a wide variety of techniques for application to particular problems. Genetics must do the same. Experiments must be conducted with animals which reproduce rapidly with a view of determining the best methods of bringing about improvement in farm animals. There should be genetical engineers—who are not geneticists out of a job, but real engineers—just as there are chemical engineers.

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PROGENY TESTING IN POULTRY BREEDING AS A MEANS OF EVALUATING THE BREEDING POTENTIALITY OF AN INDIVIDUAL[1]

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DURING the past 15 or 20 years in such widely separated countries as Australia, England and the United States, the progeny test has been applied by poultry breeders with considerable success in the development of high-laying strains. Although the application of the progeny test in the selection of breeding stock was limited to relatively few breeders in various countries, the success achieved in a number of cases has been quite phenomenal. Paradoxical as it may seem, during all these years the practical poultry breeder has shown no interest in the development of a formula for determining an index of the breeding potentiality of either the sire or the dam. In his application of the progeny test the practical breeder has been guided by a comparison of the laying performance of the daughters of different matings. Males and females for future breeding purposes have been selected from those families having the largest number of full-sisters with high records.

It seems to have remained for those interested in dairy breeding to first develop formulae for determining the relative breeding values of different sires. Among the formulae which have been developed, those of Yapp (1924), Goodale (1927), Warren (1932) and Wright (1932) all take into consideration the production of the dam in an attempt to evaluate the breeding potentiality of the sire. That such a method of determining the so-

[1] Contributed to a symposium on "The Progeny Test as a Means of Evaluating the Breeding Potentialities of the Individual," held by the Genetics Society of America at Atlantic City, N. J., December 27, 1932.

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called sire's index is not applicable in the case of breeding for egg production, where the female breeders used each year have been selected on the basis of laying a minimum of 200 eggs each during their first laying year, is made clear in subsequent observations.

It is interesting to note that Warren (1932) has suggested a formula for determining not only the index of a sire mated to a number of dams but also a formula to be applied to each mating of sire and dam. For each mating the male's breeding value is estimated by adding one half of the difference between the dam's record and the average of her daughters' records to the average of the daughters' records when the daughters' average is higher than the dam's record and by subtracting one half of the difference between the dam's record and the average of her daughters' records when the daughters' average is lower than the dam's record.

Although Warren's method of determining the breeding index of a mating may result in a more nearly correct appraisal of the breeding potentialities of the male than in the case of some of the other formulae, it has been found in the case of the Rhode Island Red dams discussed in this paper that the dam's egg production is not a factor in accounting for the differences in the average egg production of the daughters of the different matings. Moreover, it is doubtful if a poultry breeder would be justified in spending the time working out a formula for the purpose of securing an index, particularly when the actual records of egg production of the daughters of various matings apparently give sufficient information for the proper appraisal of the breeding worth of a given sire and dam. That such is the case would seem to be supported by the statement of Edwards (1932), who has emphasized the weaknesses of various sires' indices used in dairy breeding and has suggested that the average yield of the daughters of a bull is the most satisfactory indicator of a bull's transmitting ability.

In order to determine the manner in which progeny testing in poultry breeding can be used in evaluating the breeding potentiality of either sire or dam, the results secured from each of a considerable number of matings made at the U. S. Animal Husbandry Experiment Farm, Beltsville, Maryland, are presented here for discussion. The results include those secured from various Rhode Island Red males used during the breeding seasons of 1928, 1929 and 1930. Males producing relatively few breeding daughters or families of less than three full-sisters per family have been omitted; otherwise all the daughters of each dam were placed in the laying houses except those physically unfit and in rare cases a pullet with a serious standard-bred defect or a disqualification. The records of egg production for the years 1928–1929, 1929–1930 and 1930–1931 were chosen as a basis of discussion for the reason that during these laying years all daughters of various matings that were placed in the laying houses were kept throughout their first year of laying except birds which died. The first laying year in the case of each bird embraces 365 days from the date she laid her first egg.

There were 1,013 Rhode Island Red daughters produced during the three years. Mortality amounted to 9.18 per cent. and the 920 daughters that completed their first year of laying averaged 192.03 eggs each.

The environmental conditions under which the daughters were kept during the three years were as identical as it was possible to maintain. The hatching season each year occurred from March 17 to the first week in May. Housing conditions were identical, the rations fed and the methods of feeding were the same, and the general methods of management were the same. Artificial lights were used in the morning during the winter months.

Table I gives the number of the sire, the number of dams to which he was mated, the average egg production of the dams, the number of daughters produced and the average egg production of the daughters. The data in

Table I involve 19 different sires, 128 dams and 729 daughters. Each sire was from a dam that laid 200 or more eggs during her first laying year. Each dam laid 200 or more eggs during her first laying year, the dams' average production, given in Table I, being based upon first-year egg production, the dams having been bred for the first time as yearlings, although several were used in their third and fourth years.

TABLE I

THE MEAN EGG PRODUCTION OF THE DAMS MATED TO VARIOUS SIRES AND THE AVERAGE EGG PRODUCTION OF THEIR DAUGHTERS

Year	Sire No.	No. of dams	Dams' mean production	No. of daughters	Daughters' production
1928	173	8	222.75	48	219.41
"	200	6	243.00	52	192.64
"	10105	9	241.70	49	215.83
"	10102	4	207.50	16	180.25
"	10101	4	215.15	20	197.65
"	10104	5	232.00	26	198.54
1929	325	4	239.00	17	186.59
"	326	3	244.00	11	171.36
"	330	7	246.43	46	200.63
"	334	7	231.29	37	210.78
"	337	2	208.00	11	141.64
"	338	7	238.00	31	206.35
"	351	11	232.27	75	170.84
"	352	7	231.71	37	196.86
1930	330	7	250.14	38	195.21
"	334	6	241.67	32	205.16
"	338	11	250.36	60	192.35
"	368	10	230.20	58	204.55
"	363	7	239.00	44	196.61
"	369	3	252.67	21	179.48

The question might well be raised as to the validity of comparing the results of the mating of a given sire with the same or different dam or a given dam with the same or different sire in each of two years. Concerning the Rhode Island Reds discussed in this paper, it may be said that comparisons of the results secured from various matings made in the three years involved appear to be

perfectly valid. It will be recalled that the daughters produced each year were given as nearly identical environmental conditions as possible from year to year. The average egg production per bird in each of the three years was as follows:

1928	195.41
1929	184.13
1930	197.87

Although it has been determined statistically that the 1929 egg production is significantly lower than that of either 1928 or 1930, the relatively low average in 1929 is apparently chiefly due to the use of sires 326, 337 and 351, three sires that proved to be among the poorest breeders of all Rhode Island Red sires used during the three years. Moreover, the average egg production per bird in White Leghorns in each of the years 1928, 1929 and 1930 was practically the same, *viz.:* 192.17, 193.50 and 193.84, respectively.

In the breeding of various classes of live stock it has frequently been suggested that the dam's record of production is indicative of her breeding potentiality. Warren (1932) has said that "the dam's inherited tendencies for egg production are indicated by her individual egg record, but the male's tendencies are unknown." Concerning this suggestion, it is probably true that among the fowls of the universe the domestic biddy of to-day with a 200-egg record has greater potentialities for transmitting good egg production to her progeny than has a wild fowl of the bamboo jungles of India that lays about 15 eggs and then goes broody. However, in a selected group of females, selected on the basis of having laid 200 or more eggs during the first year of laying, the dam's record of egg production apparently has little or no significance, as shown by the data in Table II.

In order to eliminate the influence of the male in determining whether or not the dam's record of egg production bears any relation to the mean egg production of the dam's daughters, data from 13 pens of Rhode Island

Reds with a sufficient number of matings per pen are available. In Table II, for each pen, the mean of the mean egg production of the daughters of each dam whose egg production was *above* the mean egg production per dam for the pen is compared with the mean of the mean egg production of the daughters of each dam whose egg production was *below* the mean egg production per dam for the pen.

Since it has been urged from time to time that a female having a number of sisters with high records is more apt to transmit high egg production to her daughters than a female having a number of sisters with low records, the data have been analyzed to determine whether or not such might be the case with the selected Rhode Island Red dams under review. In Table II, for each pen, the mean of the mean egg production of the daughters of each dam whose egg production together with that of her full-sisters was *above* the mean of the mean egg production of the full-sisters of all dams in each pen is compared with the mean of the mean egg production of the daughters of each dam whose egg production, together with that of her full-sisters, was *below* the mean of the mean egg production of the full-sisters of all dams in each pen.

From the standpoint of the relationship between the record of egg production of the dam and the mean egg production of her daughters, the data in the third and fourth columns of Table II show that there was relatively little difference between the egg production of the daughters whose dam's record was *above* the mean egg production per dam for each pen and the egg production of the daughters whose dam's record was *below* the mean egg production per dam for each pen. In 6 pens out of the 13 the dams whose records were *above* the dams' mean for the pen produced daughters whose mean egg production was lower than the mean egg production of the daughters produced by dams whose records were *below* the dams' mean for the pen; in the thirteenth pen the

TABLE II

THE MEAN OF THE MEAN EGG PRODUCTION OF THE DAUGHTERS OF RHODE ISLAND RED DAMS IN EACH OF 13 PENS TREATED FROM THE STANDPOINT OF ELIMINATING THE INFLUENCE OF THE MALE IN DETERMINING THE INFLUENCE OF THE DAM'S RECORD OF EGG PRODUCTION AND IN DETERMINING THE INFLUENCE OF THE MEAN EGG PRODUCTION OF THE DAM'S FULL-SISTER FAMILY IN TRANSMITTING EGG-LAYING ABILITY

Sire	Year	The mean of the mean egg production of daughters whose dams' records were—		The mean of the mean egg production of daughters whose dams' full-sister families' records were—	
		Above the mean egg production per dam for the pen*	Below the mean egg production per dam for the pen*	Above the mean of the egg production of the full-sisters*	Below the mean of the egg production of the full-sisters*
173	1928	215	222	206	226
200	"	189	184	196	190
10105	"	214	193	204	211
338	1929	205	204	207	202
330	"	202	203	200	206
352	"	190	204	193	203
334	"	202	218	213	208
351	"	175	169	161	176
363	1930	215	175	198	197
338	"	184	199	198	175
330	"	199	194	194	198
334	"	204	215	193	216
368	"	205	205	198	207

* Decimals have been omitted.

daughters of the dams whose records were *above* the dams' mean for the pen laid the same number of eggs as the daughters of the dams whose records were *below* the dams' mean for the pen. Therefore, in this selected group of Rhode Island Red dams mated to selected sires the record of the dam does not serve as an index of her ability to transmit egg production to her daughters.

The data in the last two columns of Table II also indicate that the mean egg production of a group of full-sisters, of which the dam is one, does not serve as an index of the dam's breeding potentiality.

The correlation between the egg production of the dams and the egg production of their daughters is 0.04

$\pm$ 0.06 and the correlation between the average egg production of full-sisters of the dams and the average egg production of the daughters of the dams is 0.04 $\pm$ 0.06, neither correlation being significant.

The results secured from matings in which the same sire was mated to two different groups of dams two different years show that the average egg production of the daughters of each of the two groups of daughters was fairly uniform. Sires Nos. 330, 334 and 338 were each used in 1929 and 1930, the average egg production of the daughters produced each year being as follows (taken from Table I):

Sire No.	1929	1930
330	200.63	195.21
334	210.78	205.16
338	206.35	192.35

The difference between the mean egg production of the daughters produced in 1929 and 1930 in the case of each sire is not significant, from which it follows that the two groups of dams mated to the same sire did not differ on the average in their breeding potentialities.

TABLE III

THE MEAN EGG PRODUCTION OF DAUGHTERS OF DAMS EACH MATED TO TWO DIFFERENT SIRES

Dam No.	Dam's production	First year			Second year		
		Sire No.	No. of daughters	Daughters' mean production*	Sire No.	No. of daughters	Daughters' mean production*
5829	246	325	4	189	338	4	241
6266	251	325	5	189	338	3	188
6112	243	200	9	194	352	3	202
6238	245	200	14	203	352	6	201
6414	242	200	5	179	352	5	191
6142	242	351	9	182	368	9	220
6312	230	351	8	192	368	5	210
6407	224	351	7	194	368	8	210
6428	210	351	7	178	368	6	169

* Decimals have been omitted.

The results secured from matings in which the same dam was mated to two different sires two different years are interesting and are given in Table III.

The results given in Table III show that in some cases the daughters of a dam mated to one male have a higher mean egg production than the daughters of the same dam mated to another male, whereas another dam mated to the same two males may give opposite results.

The results secured when the same sire is mated to the same dam two years in succession show that although in most cases the mean egg production of the two groups of daughters is quite comparable, there are a few cases in which the differences are rather great. The results secured from such matings are given in Table IV.

TABLE IV

FOR EACH OF TWO YEARS THE MEAN EGG PRODUCTION OF DAUGHTERS OF THE SAME DAM MATED TO THE SAME SIRE

Sire No.	Dam No.	Dam's production	First year		Second year	
			No. of daughters	Daughters' mean production*	No. of daughters	Daughters' mean production*
173	5416	229	8	228	8	243
173	5551	214	6	213	5	205
176	6024	212	8	217	5	189
176	6027	206	6	178	4	222
330	6213	271	7	177	5	198
330	6217	254	7	220	4	192
334	6401	233	6	214	3	184
338	6462	260	6	215	7	217

* Decimals have been omitted.

If the results given in Tables III and IV are compared, it is observed that the differences between the mean egg production of the daughters produced each year by matings of the same sire × same dam are practically as large as are the differences between the mean egg production of the daughters produced each year by matings of different sire × same dam.

The data in Table IV show that since the average egg production of the daughters secured from the mating of a given sire and a given dam one year may differ considerably from the average egg production of the daughters secured from the same mating another year, the possibility of establishing a reliable index representing the breeding potentiality of either the sire or the dam seems problematical. This would seem to be especially true in the breeding of some of the larger classes of live-stock because of the relatively small number of progeny produced by most sires, to say nothing of the limited number of progeny produced by most dams. Then again, there apparently have been very few cases in which large numbers of progeny from various matings have been kept under uniform environmental conditions, as was the case with the Rhode Island Red daughters whose records are under discussion.

That full-brothers may produce significantly different results concerning the mean egg production of their daughters is shown by the results given in Table V.

TABLE V

THE MEAN EGG PRODUCTION OF DAUGHTERS OF TWO FULL-BROTHERS

Sire No.	No. of dams	Dam's mean production	No. of daughters	Daughters' mean production
200	6	243.00	52	192.64 ± 3.72
10105	9	241.70	49	215.83 ± 5.05
			Difference	23.19 ± 6.27

Although the difference in mean egg production between the two groups of daughters in Table V is significant, it is interesting to note that the mating of sire 200 × dam 6238 produced fourteen daughters whose mean egg production was 223.00 eggs, which is slightly above the mean of all daughters of 10105. It is to be noted further that the mean egg production of the daughters of sire 200 × dam 6238 exceeded the mean egg production of the daughters of six out of the nine dams mated to sire 10105.

The poultry breeder is interested not only in the mean egg production of all the daughters of each of all sires used but also in the mean egg production of the daughters of each dam. It is quite possible that the mean egg production of the daughters of a given dam may be of greater importance in the selection of future breeding stock than the mean egg production of all the daughters of the same sire to which the given dam was mated. In other words, the poultry breeder is vitally interested in the results secured from each individual mating.

The mean egg production of daughters of each two or more full-sisters mated to a different sire sometimes differ quite markedly, as shown in Table VI.

TABLE VI

THE MEAN EGG PRODUCTION OF DAUGHTERS OF EACH OF TWO FULL-SISTERS MATED TO A DIFFERENT SIRE

Dam No.*	Dam's production	Sire No.	No. of daughters	Daughters' mean production‡
5677	220	173†	4	186
5679	261	10105	3	206
5932	211	10105†	4	215
5967	226	10101	5	179
6213	271	330	7	177
6303	238	338†	7	209
6142	242	351	10	182
6218	230	334†	6	220
6144	223	200	13	178
6254	227	334†	6	215
6436	250	325	3	178
6537	245	363†	9	211
6668	271	330	8	207
6695	247	368†	3	174

* Full-sisters are shown in pairs.

† Indicates the superior sire of each pair in respect to the mean egg production of all daughters produced, as given in Table I.

‡ Decimals have been omitted.

From the standpoint of the results secured from each pair of sires mated to full-sisters, the data in Table VI indicate that in 5 cases out of 7 in which the mean egg

production of the daughters of one sire was higher, the mean egg production of all the daughters of that sire mated to various dams was also higher, as shown in Table I.

Quite different results are sometimes secured from matings of a sire to full-sisters, as shown in Table VII. The dam's egg production has been omitted in order to save space.

TABLE VII

THE MEAN EGG PRODUCTION OF DAUGHTERS OF EACH OF TWO OR MORE FULL-SISTERS MATED TO THE SAME SIRE

Sire No.	Dam No.*	No. of daughters	Daughters' mean production†	Sire No.	Dam No.*	No. of daughters	Daughters' mean production†
173	5829	8	209	338	6502	7	188
	5846	7	201		6627	4	203
	5928	5	207		6630	5	192
330	6200	10	208		6752	6	169
					6773	6	191
	6213	7	177		6792	6	204
330	6465	3	231				
	6532	6	180				
	6668	8	207	363	6537	9	211
					6577	4	178
330	6549	7	205		6735	3	166
					6750	7	221
	6844	5	159				
351	6312	8	192	368	6312	5	210
	6428	7	178		6428	6	169
352	6264	6	169	10105	5680	3	127
	6400	7	208		5923	4	214

* Dams mated to the same sire are full-sisters.

† Decimals have been omitted.

The data given in Table VII show that in some cases the mean egg production of the daughters of full-sisters mated to the same sire varied as much as 30 or more eggs. It is apparent that full-sisters selected on the basis of having laid a minimum of 200 eggs each may differ quite markedly in their breeding potentialities, irrespective of

the actual number of eggs they laid during their first year of laying. Theoretically, the logical way of determining the relative breeding potentialities of a group of full-sisters or any other group of dams would be to mate such dams to males that have the genes for egg production in a recessive condition. The difficulty of identifying males of this kind is obvious to any one who has made a study of the inheritance of such a complex character as egg-laying ability. If such were possible it might be further possible to establish the fact that the egg production, within a certain range, of selected dams is significantly correlated with breeding potentiality.

That sires may differ in their breeding potentialities is indicated by the differences in the mean egg production of their daughters, as given in Table I. The mean egg production of the daughters of the sires given in the table varied from 141.64 to 219.40, although in a number of cases the differences in the mean egg production are not significant, as, for instance, the daughters of sire No. 10101 with a mean egg production of 197.65 and the daughters of sire No. 10104 with a mean egg production of 198.54. It is true that the number of daughters of certain sires is too small to attach much significance to their mean egg production. However, in order to determine whether or not the difference between the mean egg production of the daughters of certain sires is significant, the results secured from three sires with relatively large

TABLE VIII

THE SIGNIFICANCE OF THE DIFFERENCE IN THE MEAN EGG PRODUCTION OF THE DAUGHTERS OF EACH OF THREE SIRES

Sire No.	No. of daughters	Daughters' mean production	Sire No.	No. of daughters	Daughters' mean production	Difference
173	48	219.41 ± 4.74	351	75	170.84 ± 3.58	48.57 ± 5.94
173	48	219.41 ± 4.74	338	60	192.35 ± 3.90	27.06 ± 6.14
338	60	192.35 ± 3.90	351	75	170.84 ± 3.58	21.51 ± 5.29

families have been analyzed and the data are presented in Table VIII.

The data in the last column of Table VIII show that the difference in the mean egg production between the daughters of each pair of sires is significant, indicating that the three sires differ among themselves concerning their breeding potentialities. A proper appraisal of the breeding potentiality of each sire would be possible if he could be mated to dams having the same genes for egg production in a recessive condition.

In conclusion, the results secured from various matings of Rhode Island Red sires, whose dams laid a minimum of 200 eggs each during their first laying year, and dams which laid a minimum of 200 eggs each during their first laying year seem to justify the following observations:

(1) The number of eggs laid by the dam could not be used as a criterion of her breeding potentialities.

(2) Therefore, in the case of this selected group of dams, their first-year records of egg production should not be used in the determination of a sire's breeding index.

(3) The mean egg production of full-sisters could not be used as an index of the breeding potentialities of any of the full-sisters.

(4) At the same time, various dams, even full-sisters, may apparently differ among themselves in their breeding potentialities.

(5) Also full-brothers may differ among themselves in their breeding potentialities.

(6) Since certain sires have been shown to differ among themselves in their breeding potentialities, it follows that the mean egg production of each sire's daughters serves as the most readily available index of a given sire's breeding potentiality.

(7) In addition, the mean egg production of the daughters of the mating of a given sire and a given dam is the index of greatest value in determining the breeding potentiality of an individual sire or dam.

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THE PROGENY TEST AND METHODS OF BREEDING APPROPRIATE TO CERTAIN SPECIES OF CROP PLANTS[1]

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REPEATED attempts by plant breeders, working with different species of both self-fertilized and cross-fertilized crops, have failed to discover any sound basis for selection of parent plants except that which involves a progeny test. With self-fertilized crops the progeny test may be directly applied because such plants reproduce with fidelity and there is no appreciable loss of vigor from one generation to the next. In the cross-fertilized crops, however, the question of how to utilize the progeny test to best advantage has not been clarified by investigation and it is somewhat complicated by fundamental differences in the breeding behavior of species as well as the nature of problems which confront the breeder of these crops. Everything considered, we believe that although our method of dealing with this topic may be somewhat indirect, most good will come from a general discussion of breeding methods in relation to species and objectives and by confining our attention to the normally cross-fertilized crops. We will then consider briefly some aspects of the progeny test in its practical application.

Let us consider first the improvement of herbage plants in general and certain legumes and grasses in particular. Discussion will be facilitated by selecting a typical problem from among the many which are likely to engage the attention of plant breeders in their efforts to improve these crops. Perhaps no more important objective could be chosen than that of developing a superior strain for grazing purposes.

[1] Contributed to a symposium on "The Progeny Test as a Means of Evaluating the Breeding Potentialities of the Individual," held by the Genetics Society of America at Atlantic City, New Jersey, December 27, 1932.

Species of herbage plants are sometimes grown in pure cultures but more often in simple or complex mixtures. In order to secure good establishment and a dense sward for pasture purposes, the seed is sown thickly. This results in intensive competition between species and even between plants of the same species. Dominance of one species over another is profoundly influenced by climatic, edaphic and biotic factors. Growth can be influenced differentially by the application of fertilizers and methods of grazing, but unless a strain is well adapted to its environment, it will fail to hold its own or compete successfully with inferior volunteer species and weedy plants.

To say that a variety or strain possesses a high degree of adaptation for pasture purposes implies that it possesses the necessary physiological and morphological characteristics which fit it for a particular environment. The requirements are exacting and frequently complex. In addition to good yield under favorable conditions there may be included drought resistance, winter hardiness, longevity or resistance to certain diseases. To these may be added those characters which directly affect its utility, as, for example, a satisfactory nutrient content and palatability, and early or late maturity. There must also be a nice balance between production of herbage and yield of seed, since one tends to develop at the expense of the other.

Having considered in a general way the nature of the problem involved in producing a new variety for pasture purposes, we are now in a position to state more precisely what are the essential qualities which such a strain should possess. First and foremost it must possess the greatest possible range of adaptation so that its usefulness will not be too greatly restricted; secondly, it must be composed of plants of the required type for pasture purposes; and finally it must be as productive as possible of high quality herbage, consistent with satisfactory seeding habits.

What methods are available to the plant breeder for developing these improved strains and what procedure is likely to be most direct and effective? These may be con-

sidered conveniently under three headings as follows: (1) selfed line breeding, (2) strain building, (3) mass selection.

Selfed Line Breeding

The method of breeding cross-fertilized plants which involves selection within selfed lines and subsequent hybridization has been widely applied in corn breeding. It is generally recognized by plant breeders as a genetically sound basis for corn improvement. Experimental evidence seems to show that it offers the best opportunity for obtaining substantial improvement in the yield of this crop. Richey (8) and others have reviewed the literature and presented comprehensive discussions covering all phases of the subject.

It must be recognized, however, that selfed line breeding has distinct limitations when applied to most other cross-fertilized crops. In many respects the corn crop lends itself particularly well to inbreeding and the utilization of selfed lines. Its mode of reproduction makes it possible to produce selfed seed and hybrid seed with a minimum of difficulty and expense. With respect to ease of manipulation it is far superior to any other of the cross-fertilized crops. The physical difficulties involved in selfing large numbers of plants in most of the herbage species is a problem that must be recognized, and the same applies to the production of hybrid seed.

While single and double crosses between selfed lines have materially increased the production of corn, it is worthy of note that the synthesizing of several selfed lines to form a new strain has not been equally productive of increased yields. This has also been found to be true in the case of rye. Evidently a general increase in yields as a result of selfed line breeding will have to come through the use of hybrid seed produced annually for field planting. This practise would be out of the question with any of the species of herbage plants. Selfed lines in these crops of necessity would have to be utilized in the form of synthetic varieties.

Inbreeding results in loss of vigor in nearly all species of herbage plants that are normally cross-fertilized. This applies to alfalfa, red clover, timothy, orchard grass, perennial rye grass, and many others. Since it does not appear that it will ever be possible to capitalize on hybrid vigor in these species through the use of F_1 seed, and since selfing is accompanied by pronounced loss in vigor of growth, the question arises as to how far this loss in vigor can be recovered in synthetic strains produced by controlled mating or random crossing of selfed lines.

Even if experience should show that maximum vigor can be restored and maintained under experimental conditions by selfed line breeding, it is altogether likely that other factors will be lost in the process, factors which may influence profoundly the physiological response of the strain to the natural environment. Where natural adaptation and ability to compete with other species is of first consideration, loss of some of the essential physiological factors which characterized the parent material should be a matter of serious concern. It is quite conceivable that the best way to secure strains of herbage plants which are capable of standing up under the varied conditions to which they will be subjected is to bring together as wide a range of selected genotypes as possible. Experience has shown that improved strains of grasses which trace their origin to single plant selections have proved disappointing when tested in places remote from those in which they originated. On the other hand, there are a considerable number of very useful strains which have originated through a process of natural selection, as, for example, Grimm alfalfa in America, Ultuna red clover in Sweden, Akaora cocksfoot and Hawke's Bay perennial rye grass in New Zealand, and Kentish wild white clover in England.

STRAIN BUILDING

The term "strain building" was first coined by Jenkin (2) to describe the methods which he employed in breed-

ing perennial rye grass. It was used by him in a very broad sense to include any system of mating by which a strain is built up by crossing from carefully selected plants. We will use the term in this sense also and as such it is to be distinguished from "Selfed line breeding," which presupposes several generations of inbreeding until the parent plants are reasonably homozygous. At the same time "strain building" does not exclude inbreeding entirely such as occurs, for example, in backcrosses. In other words, it may be thought of as comparable to live-stock breeding where foundation stock is selected on type and performance both of the parents and their progenies.

The method of "strain building" involves the composite crossing of few or many carefully selected parent plants. The number of plants contributing to the new strain will depend to a considerable extent on the number of unrelated individuals available which possess the necessary qualifications, and this in turn will depend in practise on the nature of the problem. If the objective is primarily the production of a persistent leafy pasture strain, as in the present case, one has only to select for growth form and productivity within the population of an appropriate habitat, in which case there is likely to be no lack of parent material. On the other hand, if it is desired to breed for some special attribute which is of comparatively rare occurrence in the species, it will be necessary to choose only those plants as parents which possess the character or characters in question. This may restrict the basis of the strain to a very few plants. Under these circumstances some degree of inbreeding is inevitable. It may even be advisable to practise repeated selfing in order to secure homozygosity as quickly as possible but it should be recognized that this will be done at the expense of vigor of growth and possibly other factors of economic importance. Very frequently, also, inbreeding results in partial or complete self-sterility, in which case out-crossing is the only alternative.

"Strain building" may be regarded as a breeding procedure directed essentially toward concentrating certain morphological or physiological characters in a particular strain. It does not necessarily contemplate complete uniformity but aims rather to increase the proportion of individuals in the population that possess the desired characteristics. The ideal, of course, is complete homozygosity but as Stapledon (9) has suggested, "the economic breeder of herbage plants may hope to achieve valuable results without necessarily becoming a slave to the idea of genetical purity."

As outlined above, the method is very broad in its application. It admits of different systems of mating and various methods of selecting parent plants. It aims to maintain vigor, as far as this is consistent with progress toward the desired result, by bringing into the strain as wide a range of genotypes as possible. The method, however, presupposes the conscious selection of parent plants as foundation stock and systematic selection within families as a basis for further crossing. In evaluating the breeding potentialities of the parent plants there can be no better guide than that obtained from a study of the progenies which they produce when mated with other individuals.

MASS SELECTION

Studies by Turesson (11) and others have shown conclusively that there exist within the species definite hereditary habitat types and that the habitat type represents the genotypical response of the species-population to a particular set of environmental conditions. They have also shown that the individuals which compose these habitat types, or "ecotypes" as they are called by Turesson, tend to be phenotypically uniform but genetically more or less heterogeneous, depending on the stability of the habitat. Climate plays the leading rôle as a modifying agent, but other factors also exert a very great influence on the character of the population, such as soil type and the effect produced by close grazing. There is

ample justification for the contention that mass selection properly employed offers a ready means of capitalizing on the work which nature has accomplished through natural selection over long periods of time. This is particularly true in the case of grasses and legumes and especially those which are required for pasture purposes. Long-continued grazing of old pastures has been shown to operate as a modifying agent to produce a race of growth-forms especially suited to a pasture habitat. It is to be expected that such a habitat will provide the best possible source of foundation plants with which to build an improved pasture strain. There is reason to believe also that when mass selection methods are adopted, the larger the number of suitable parent plants that can be brought into the strain the better, and that special methods should be adopted to insure the greatest possible degree of random-pollination.

Selfed-Line Breeding vs. Strain Building

The method of breeding which one chooses to adopt with any particular species will be dictated very largely by the breeding behavior of the species with respect to fertility relationships and the degree to which the plants are reduced in vigor by selfing. In this connection it may be profitable to consider very briefly these two factors in a few of the major crop plants and how they are likely to influence the choice of appropriate breeding methods.

Alfalfa: Alfalfa plants, for the most part, are cross-fertilized, but they are also, to a considerable extent, self-fertilized. The total quantity of seed produced and the relative amount of selfing under field conditions is profoundly influenced by weather conditions at the time of pollination. Alfalfa is moderately self-fertile when artificially self-pollinated. Inbreeding is accompanied by a very marked reduction in self-fertility which is out of all proportion to the very considerable decrease in vegetative growth.

The writer (5, 6) has conducted experiments with alfalfa for the past ten years, primarily to determine the

effects of selfed line breeding and its possibilities as a practical method of improvement. The most conspicuous result of inbreeding was seen to be a marked reduction in vigor and seed production. This could be observed up to and including the fourth generation.

The results of selfed line breeding with alfalfa in these experiments have not been impressive as a practical method of improvement. In addition to the physical difficulty of handling more than a few score selfed lines, there is the problem of greatly reduced fertility. This amounted to 70 per cent. in the second generation, and in the fourth, almost complete self-sterility in a large proportion of the families. Williams (15) found that the average yield of seed from first generation selfed lines was only 12.4 per cent. of that of the parent plants from which they were derived.

Not only is self-fertility greatly reduced by inbreeding, but cross-fertility also appears to be much less. Our results show that where 65 fourth generation selfed lines were grown together in a compact field under conditions favorable for cross-pollination, with the standard variety in every fourth row, the average seed yield of the inbred families was only 22 per cent. of the standard variety. Vigor of growth, on the other hand, as measured by total yield of plants, was reduced to only 54 per cent. This emphasizes the marked effect of inbreeding on fertility.

We are now attempting to develop seed production from another angle which appears quite promising. Five unrelated mother plants from a highly adapted variety are available which produce a normal crop of seed without artificial manipulation or the visitation of insects. One of these plants has matured five crops of seed under a variety of conditions (field and greenhouse) and a full quota of pods have always been secured. This family has been inbred to the third generation with consequent loss in vigor. Seed production has been so seriously impaired that it has become necessary to abandon selfing and resort to out-crossing with the other plants. By inter-crossing and back-crossing

it should be possible to attain homozygosity of the factors involved without much loss in vigor, providing the character is inherited in a simple manner. Otherwise a larger number of suitable mother plants will be necessary.

The difficulties which have been mentioned when selfed line breeding is adopted with alfalfa suggests that "strain building" is likely to be the better method. This conclusion is illustrated beautifully by the problem stated above in connection with developing a strain of alfalfa which is highly self-fertile and also self-pollinating. It is typical of a large class of problems that may be encountered in the breeding of cross-fertilized crops. Among these may be mentioned the breeding of a disease-resistant strain, when resistant parent plants are of rare occurrence. On the other hand it is not so difficult to produce strains which reproduce themselves with comparative purity for specialized growth-forms because plants of a given type are usually fairly abundant, in which case it is far more important to adopt a method of breeding which will maintain maximum vigor than to attain genetical purity.

Red clover: Self-sterility in red clover is a physiological phenomenon due to the inhibiting action of the stylar tissue. Williams (14) concludes that this species, for all practical purposes, can be regarded as being self-sterile. This view appears to be amply justified by the facts. He states also that loss of vigor resulting from inbreeding presents even greater difficulties in the improvement of red clover than cross-incompatibility. The reduction was found to be very pronounced in the second generation, becoming less at each subsequent crossing until the fourth or fifth generation was reached, after which there was no apparent loss. The average loss in vigor in the first to the third generation was given as 50 to 60 per cent. Inbreeding, however, except in so far as it decreased the chances of cross-fertilization, had no direct effect on fertility or on the size and quality of the seed. It would seem from this that red clover is dis-

tinctly different from alfalfa with respect to the effect of inbreeding on seed production.

Red clover appears to be an example of a very important species of cross-fertilized crop which can best be improved by composite crossing. Of necessity, a method of breeding must be adopted which aims to utilize parent plants which are qualified to contribute particular genetic factors, where genetic purity is required, or those which are phenotypically similar where the chief consideration is ecotypic homogeneity of the strain aggregate.

Perennial grasses: It is unnecessary for our purpose to discuss at any great length the breeding behavior of the different cultivated grasses, except to survey very briefly the behavior of a few important economic species in relation to fertility and vegetative vigor under conditions of selfing and crossing.

Valle (12) investigated the tall Finnish type of timothy with reference to the effects of inbreeding and concluded that the selfing method can not lead to practical results. He was unable to obtain any constant self-fertile lines, and inbreeding resulted in loss of vigor. Self-sterility was found to increase progressively with continued selfing. Jenkin (4) studied self-fertility in fifty plants of the semi-hay type of timothy. Forty-three of these were of very low fertility, yielding less than one seed per centimeter of inflorescence. On the other hand, a few plants were very highly self-fertile. These results agree in general with those of other workers.

In a study of over 1,200 plants of orchard grass, *Dactylis glomerata,* which were selfed, Stapledon (10) found that the degree of self-fertility varied from absolute self-fertility to apparent complete self-fertility. On the average, plants of orchard grass were found to be about half as vigorous when derived from selfing as when obtained by hybridization.

The results of fertility studies in perennial rye grass, *Lolium perenne,* have been presented by Jenkin (33). These emphasize the low degree of self-fertility in this species. It was estimated that 50 per cent. of the plants

set less than 1 per cent. of the possible number of seeds, while 75 per cent. of the plants set less than 3 per cent. Only in two plants per hundred was seed setting greater than 20 per cent., or one seed per spikelet. These results are in general agreement with those reported by Gregor (1). With respect to loss in vigor due to selfing, Jenkin reports that reduction in yield is well over 40 per cent. on the average as compared with that produced by intercrossing.

The writer has conducted breeding experiments with awnless brome grass, *Bromus inermis,* for the past ten years in which 100 selfed lines were grown in each of four generations. Self-sterility has increased in each generation and much loss in vigor has taken place. This decrease in yield was not very apparent until the third generation, but in the fourth it became very pronounced.

The findings which we have summarized from the work of several investigators on four important economic grasses emphasize how wide-spread are the deleterious effects of inbreeding in cross-fertilized crops. These in turn have a very important bearing on breeding procedure, as has been pointed out in connection with the other species previously discussed.

Potatoes: There are some interesting features of the potato crop and potato breeding which are worth mentioning in connection with the relative value of "selfed line breeding" and "strain breeding" methods. Although the potato plant is normally self-fertilized, the cultivated strains are extremely heterozygous, due to the fact that they originated as hybrids and are propagated from tubers. With respect to ease of self- and cross-pollination and mode of propagation, the potato is especially well suited to selfed line breeding because all the hybrid vigor which results from the crossing of superior selfed lines can be retained, since segregation in subsequent generations is avoided by vegetative propagation. Loss in vigor due to inbreeding, although very pronounced in the potato, is not in itself a serious drawback, for reasons already given. Pollen sterility, on the other

hand, presents a difficulty of some magnitude, since it is almost complete in the major economic varieties. The problem of securing viable pollen, however, is probably at least as great, whether the method adopted be outcrossing between unrelated plants or systematic inbreeding. Everything considered, therefore, on theoretical grounds, it might be expected that the method of "selection within self-fertilized lines" should find its most ideal application in the breeding of potatoes. This view is strongly supported by Krantz (7).

There is one angle to the question, however, which remains an unknown quantity as far as success in the breeding of economic varieties of potatoes is concerned, namely, the effect which continuous inbreeding may have by restricting the genetic constitutions of the plants and thus narrowing their range of adaptation. Since many factors of physiological significance probably can not be measured in terms of hybrid vigor, it is reasonable to suppose that some of them may be lost through inbreeding. On these grounds we are justified in awaiting the verdict of conclusive experimental evidence to show that strains of potatoes, and other cross-fertilized crops, produced by the method of selfed line breeding, possess the necessary stamina to meet the rough and tumble of practical farm conditions. It is well known that many otherwise admirable varieties of crop plants have not measured up to this test, and it is at least debatable whether their failure may not have been due to a too much restricted inheritance. On the other hand, it is not difficult to name many varieties of crop plants, including potatoes, with a remarkably wide range of adaptation, which originated either from very wide crosses or composite crossing.

Having pointed out that selfed line breeding is especially applicable to the potato crop and having suggested a possible limitation of that method of improvement, we can now go further and say that the potato plant should provide exceptionally good material for studying the

differential effects of inbreeding as between vigor and other physiological qualities of practical importance. Because of the fact that maximum hybrid vigor can be retained by vegetative propagation, a conspicuous lack of adaptive response to differences of environment, beyond that which would normally occur with standard sorts, may logically be attributed to inbreeding.

The Progeny Test

Having considered methods of breeding in relation to the practical improvement of cross-fertilized crop plants, a few observations may be added with reference to the progeny test in its practical application.

It may be taken for granted that the progeny test in one form or another provides the only method of evaluating the breeding potentialities of an individual. The progeny may be produced from selfed seed or from hybrid seed of crosses between homozygous or heterozygous individuals. With all these three classes of parent material the progeny test is extensively employed, but the information obtained in each case differs greatly in significance and precision.

When the progeny test is conducted with selfed seed of heterozygous plants, it is easy to measure the relative vigor of growth, but this information, if obtained in the actively segregating generations, is of very little value. This was clearly demonstrated in experiments by the writer with both alfalfa and brome grass. It was found that very pronounced loss in vigor may occur in one of the first four or five generations of inbreeding. A striking example may be cited to illustrate this point. One "original" parent plant of alfalfa produced a very vigorous first generation progeny and four excellent second generation selfed lines. The latter were regarded as the best out of about 80 progenies in this project. These were again self-fertilized, but all the third generation selfed lines were almost too weak to survive, although sixteen of them were grown.

Results such as these were not infrequent, but nevertheless high yielding first generation progenies, on the average, tended to produce the most vigorous selfed lines in succeeding generations. Exceptions, however, were so numerous as to make the progeny test ineffective when vigor of growth was taken as a basis of selection.

With respect to phenotypic selection, our experience has been that progeny tests can be used to considerable advantage. In general, the first generation selfed lines of alfalfa gave a fair indication of growth-form and also the extent to which parent plants will breed true for a particular type. Although segregation takes place for many morphological characters in nearly all selfed lines, successive generations tend to exhibit the same general characteristics in a fair proportion of families. It is possible, therefore, to eliminate a considerable number of "original" parent plants on the basis of general appearance in first and second generation selfed lines.

The second class of progeny tests referred to above is that in which hybrid seed from homozygous parents is used, as in the case of single crosses between selfed lines of corn. In this case where the parents are required for the production of F_1 seed, the progeny test provides a direct method of evaluating the breeding potentialities and all other characters of economic importance. F_1 hybrids provide also the best indication that we have of the value of parent plants in composite crossing, but for this purpose such progeny tests are not necessarily reliable.

The third class of progeny tests is that in which heterozygous parent plants, when inter-crossed, are evaluated on the performance of their progenies. Such a procedure is necessary in the breeding of red clover, since here cross-fertilization is practically obligatory. In this case the plants are extremely heterozygous. Williams (13) successfully employs the progeny test with this species. Carefully selected plants of similar type are paired and mated in various combinations. Those which consistently produce high yielding and otherwise desirable progenies when out-crossed with other individuals are

labeled as good parents. This is the method employed by animal breeders. There seems no good reason why it should not be practised by plant breeders wherever selfed line breeding may be found impossible or undesirable.

One thing in particular relating to the progeny test deserves special emphasis. This is the supreme importance of conducting such tests under environmental conditions similar to those in which the variety presumably will be grown. Plant breeding must be initiated at certain centers but it is a great advantage if promising strains in the making can be subjected to the incidence of extremes of temperature, drought, disease organisms or whatever factors may influence the success of the new production. Attempts have been made to simulate nature by providing artificial conditions in the laboratory for conducting progeny tests, and these have been moderately successful in certain cases, but generally speaking few tests have yet been devised which approximate natural conditions. More rapid progress in this direction would greatly facilitate the work of the plant breeders.

Summary

Methods of procedure in breeding self-fertilized species of crop plants have been fairly well standardized. The same can not be said with reference to cross-fertilized crops. The latter include such widely different species as corn, alfalfa, red clover, timothy and many other grasses and legumes. These vary greatly in their mode of reproduction and breeding behavior. Improvement of these species presents a variety of problems, depending on how they are to be cultured and utilized. Methods of breeding should be used, which are appropriate to the species concerned and the objective to be attained.

Breeding methods commonly employed can be grouped under three headings—selfed line breeding, strain building and mass selection. These are discussed and compared with respect to their applicability to different species and specific problems.

"Selfed line breeding" has been employed most extensively in corn improvement. Although apparently well adapted to this crop, it has only a limited usefulness in the breeding of herbage plants.

"Strain building" involves the crossing of few or many carefully selected parent plants. It admits of different systems of mating and aims to maintain vigor of growth by bringing into the strain as wide a range of genotypes as possible, as far as this is consistent with progress toward the desired result. Inbreeding may be detrimental in so far as it tends to narrow the lines of inheritance and restrict the range of adaptation of the strain.

In nature there exists within the species definite hereditary habitat types which represent the genotypical response of the species-population to a particular habitat. "Mass selection" provides a ready means of capitalizing on the work which nature has accomplished.

The progeny test provides the only reliable method of evaluating the breeding potentialities of parent plants. The information to be gained from such tests differs greatly in significance and precision depending on whether the progeny is grown from selfed seed or from hybrid seed of crosses between homozygous or heterozygous individuals. It is of supreme importance that progenies shall be subjected to the incidence of those environmental factors which presumably may influence the success of the new production.

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PROGRESSIVE MUTATIONS INDUCED IN *GOSSYPIUM HIRSUTUM* BY RADIATIONS[1]

W. R. HORLACHER AND D. T. KILLOUGH[2]

GENE mutations in both directions at a single locus have been reported by Patterson and Muller (1930), Hanson (1928), and Timofeeff-Ressovsky (1929a, 1929b, 1931) as having been produced in Drosophila by radiations. Stadler (1931) has noted similar phenomena in maize. These cases are important because of the evidence they present that recessive mutations are not losses of genes and because they show that mutations which are beneficial to the organism, progressive mutations, can arise.

Two progressive mutations have been induced by radiations in cotton (*Gossypium hirsutum*). The evidence that these mutations had occurred in the somatic tissues of cotton plants grown from x-rayed seeds was presented in a recent paper (Horlacher and Killough, 1931). Breeding evidence has now been secured to show that both of these mutations are transmitted to succeeding generations.

The first of the progressive mutations to be discussed is the one from forked leaf shape to normal leaf shape. Seeds containing embryos known to be heterozygous for leaf shape were x-rayed and plants grown from these. The bolls from these plants were selfed and the individual boll progeny grown separately. Normal segregation for leaf shape gives 1 normal leaf: 2 intermediate leaf: 1 forked leaf. A mutation from forked to normal in a branch of the heterozygous plant (*Nn* to *NN*) would produce

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a boll from which all the progeny would have normal leaf shape. Likewise a mutation from normal to forked (*Nn* to *nn*) would produce a boll from which all the progeny would have forked leaves. A total of 529 individual boll progenies were grown. Among these a number of bolls produced only normal leaf progeny and a few produced only forked leaf progeny. These results are shown in detail in Table 1.

TABLE 1

No. of bolls	Plants from each boll			Odds against this being a chance deviation from the 1:2:1 ratio
	Normal leaf	Intermediate leaf	Forked leaf	
2	8	0	0	65,535:1
1	5	0	0	1,023:1
4	4	0	0	255:1
4	3	0	0	63:1
10	2	0	0	15:1
28	1	0	0	3:1
1	0	0	3	63:1
6	0	0	2	15:1
15	0	0	1	3:1

The two bolls having 8 normal leaf plants each are very highly indicative of a mutation from *n* to *N* in each case. The other bolls furnish supporting evidence. Selfed bolls from these normal leaf plants have been found to produce 100 per cent. normal leaf progeny. This proves that these plants are homozygous. Of the 49 bolls listed in Table 1 as producing only normal leaf plants, 8 were from plant 1–59. This plant had one other boll which gave 9 normal leaf and 7 intermediate leaf progeny. Five more of the bolls producing only normal leaf progeny were from plant 1–50. This plant had 9 other bolls, which segregated for the different leaf shapes. These two plants produced all the bolls which gave 4 or more progeny all of which had normal leaf shape. They both furnish good evidence that a mutation has been produced from forked leaf to normal leaf shape.

Selfed seed from these normal leaf plants have produced all normal leaf progeny. None of the 22 bolls listed in Table 1 as producing only forked leaf progeny produced a large enough number of offspring to give good evidence that a mutation had been produced from normal leaf to forked leaf. They are included here, however, as giving some indication of the possibility of producing mutations in both directions at this locus.

There are two other possible explanations of the production of the bolls giving 100 per cent. normal leaf progeny by the x-ray treatment of the heterozygous seeds. The first is that the radiation has caused a deletion of the chromosome carrying the gene *n* for forked leaf. This would leave the plant monosomic for the chromosome carrying the gene *N* for normal leaf. In that case all the functional gametes would probably carry the chromosome with *N* and would produce only normal leaf progeny. The same reasoning would apply in case there was a deletion of only that portion of the chromosome carrying the gene *n*.

The other possible explanation of this variation is that a gametic lethal which is closely linked with *n* has been induced. The genetic constitution of the plant under this condition would be (*NL*)(*nl*), *l* representing the gametic lethal. The only functional gametes produced would be *NL*. The union of two of these, (*NL*)(*NL*), would produce normal leaf progeny and that would be the only type of progeny produced by a boll coming from such tissue.

Evidence for the production of a mutation from forked leaf to normal leaf has also been secured from another source. This case does not lend itself to interpretation by either of the two alternative hypotheses suggested above because the gene *N* for normal leaf was not in this stock before it was irradiated. Plant No. 30–41, grown from an x-rayed seed of homozygous forked leaf cotton, produced 6 bolls, 5 of which gave forked and intermediate leaf progeny, while the other boll (B5) gave 1 normal

and 2 intermediate leaf progeny. The intermediate leaf progeny may represent in some cases variants within the homozygous forked genotype, but in other cases they may be the result of gene changes. The normal leaf progeny, however, could have resulted only from a mutation, as even an accidental cross pollination of a forked leaf plant by a normal leaf plant would result in the production of intermediate leaf shape. There are, thus, three cases of induced mutations of the forked leaf gene to its allelomorph, the normal leaf gene. These constitute mutations in fewer than one per cent. of the seeds x-rayed.

The normal leaf has much more leaf surface than does the forked leaf. In the normal leaf the lobes are broad and the indentations between the lobes are not very deep. The lobes of the forked leaf are very narrow, almost pencil-like, and the indentations are very deep. The normal leaf, therefore, provides the plant with more food-making surface than does the forked leaf. Considered on this basis, the mutation from forked leaf to normal leaf is progressive.

The other progressive mutation is the one from virescent yellow leaf and plant color to normal green. Virescent yellow cotton does not have as much chlorophyll as does normal green cotton. The yellow pigment which is normally present in all cotton plants shows along with the reduced amount of chlorophyll which is found in these plants giving the characteristic virescent yellow color to these plants. This cotton does not grow as tall as normal green cotton, neither does it yield as much lint cotton per plant.

The virescent yellow mutant character was obtained from R. E. Karper and R. E. Dickson, who discovered two plants of this type in a large field of Mebane cotton on the Experiment Station at Spur, Texas, in 1925. Only two plants with this characteristic appeared in this field. Virescent yellow was a type hitherto unknown and it appears likely that these virescent yellow plants were the result of a mutation. Subsequent tests by Killough

(1929) showed these two plants to be homozygous virescent yellow (*vv*) and a simple recessive to green. He reported a ratio of 545 green to 177 virescent yellow in the segregating generation.

Several hundred seeds of virescent yellow cotton were x-rayed. A considerable percentage of the plants grown from these seeds had green areas of greater or less extent. From self-fertilized flowers on some of the plants with green areas 66 progeny were grown. Of these, 13 were normal green plants. These 13 green plants came from four different bolls. The fact that these green plants developed from self-fertilized bolls of virescent yellow cotton grown from x-rayed seed is good evidence that they resulted from induced mutation and not from cross pollination. In order to secure further proof that these green plants were due to induced mutations and not to accidental cross pollinations, flowers on these plants were selfed and progeny grown therefrom. If cross pollination had occurred all of the green plants would of necessity be heterozygous and the progeny would segregate in the ratio of 3 green to 1 virescent yellow. If the green plants were due to mutations, however, an occasional homozygous green plant might be expected in this group, although the majority of the green plants resulting from induced mutations would be heterozygous. The occurrence of a homozygous green plant would be definite proof of an induced mutation. One of the 13 green plants produced 21 green and no virescent yellow progeny. This plant was undoubtedly homozygous green, as the odds against the chance production of 21 dominants and no recessives by a heterozygous plant are 420:1. The other 12 of these 13 plants proved to be heterozygous.

Proof that a mutation has been induced by radiations from virescent yellow to green is shown by the facts that (1) 13 green plants arose from self-fertilized bolls of irradiated virescent yellow cotton, (2) one of these 13 green plants was homozygous green, and (3) green

plants have never arisen from virescent yellow under any other conditions.

The mutation rate from virescent yellow to green was less than one per cent.

The green plants resulting from the induced mutations from virescent yellow to green were larger, thriftier and more vigorous than the virescent yellow plants from the same bolls. It is advantageous to the plant to have the amount of chlorophyll that is present in the normal green plant rather than the amount that is in virescent yellow cotton. This mutation may, therefore, also be considered as progressive.

Another important consideration regarding this mutation is that it is the reversal of a mutation that had previously occurred in nature. Virescent yellow, as pointed out above, undoubtedly arose as a natural mutation from green. This gene has later mutated back to green under the influence of radiations.

Summary

Mutations which are progressive have been produced in cotton (*Gossypium hirsutum*) by x-ray treatment of the dry seeds. These mutations consist of:

1. A mutation from forked leaf shape to normal leaf shape. This was induced in two different lines of cotton, *viz.*,
   a. An F_1 which was heterozygous, *Nn*.
   b. A homozygous forked leaf line, *nn*.
2. A mutation from virescent yellow leaf and plant color to normal green leaf and plant color.

The mutation rate in each case was less than one per cent.

Evidence is also presented for reversible mutations in cotton. There are indications that a mutation has been induced from normal leaf to forked leaf, the reverse of the mutation from forked leaf to normal leaf. The induced mutation from virescent yellow to green is the

reversal of the mutation from green to virescent yellow which had previously occurred in nature.

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CROSSING PRODUCTION AND EXHIBITION RHODE ISLAND REDS[1]

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EXHIBITION-BRED Rhode Island Red chicks were hatched and reared with pedigreed production-bred chicks in the spring of 1929. The former group was hatched from eggs furnished by one of the leading breeders of the world. The pedigreed chicks had an ancestry that had been selected and bred for high fecundity at the Massachusetts Agricultural Experiment Station since 1913. The two groups of chicks differed widely in plumage color, to some extent in rate of growth and to a marked degree in age at which sexual maturity was attained. Crosses were made in 1930 between these two types and this report concerns itself with some of the results in F_1 and F_2 with respect to characteristics affecting annual egg production.

Goodale and Sanborn (1922) pointed out that the number of eggs laid in a year depends very largely upon age at sexual maturity, winter pause, high intensity, broodiness and persistency. Hays and Sanborn (1927) have shown the net relation of each of these five traits to annual egg record. Hays (1924) reports the mode of inheritance of the first four and Hays (1927) reports on the inheritance of persistency. In general, the highest producer must carry these five desirable inherited traits and the true-breeding high producer will have the following genetic formula: $E_0E'EmmIII'I'aaccPP$.

SEXUAL MATURITY

The approach of sexual maturity in the individual is definitely recognizable in the female by the laying of eggs. In the male no specific criterion of sexual maturity is recognized. There are, however, certain external

[1] Paper presented before the Sixth International Congress of Genetics, Ithaca, N. Y., 1932.

changes which suggest that the male is sexually mature and may reproduce. Such secondary sexual characters as the adult male type of comb, the male type of adult plumage and the beginning of spur development probably indicate complete sexual maturity. But these secondary characters are relative only and as such can not be measured in relation to the appearance of functional spermatozoa in the male reproductive system. This report will, therefore, deal only with female descendants.

Early sexual maturity has been shown to be associated with high annual egg production by Rice (1915), Hurst (1921), Kempster (1922, 1925, 1926 and 1927), Ball and Alder (1917), Kennard (1921), Hays, Sanborn and James (1924), Jull (1923 and 1924), Parkhurst and Buster (1927), Knox (1930) and others. Hays and Sanborn (1927b, *loc. cit.*) showed, however, that early sexual maturity as such did not affect annual egg production but that early maturity affects production because it is associated with high intensity and very intimately associated with high persistency. Hays (1927) pointed out the linkage between gene E′ for early maturity and gene P for high persistency.

TABLE 1

SEXUAL MATURITY

Exhibition Sire J 711 (Eee′e′)	Production Dams (Early)			
	J 1683 (EoE′e′)	J 2247 (EoE′e′)	J 2662 (Eoe′e′)	J 2666 (EoE′e′)
	F_1 Daughters			
	36 Early 18 Late			
	F_2 Daughters			
18 Early 22 Late		3 Early 13 Late		

Phenotypically early maturing pullets begin laying at 215 days or younger, late maturing at 216 days or older.

P_1 dams were all phenotypically early and, mated to an exhibition male, gave 36 early and 18 late daughters.

Early maturing F_1 dams mated to F_1 males (two used) gave 18 early and 22 late.

Late maturing F_1 dams mated to one F_1 male gave 3 early and 13 late.

These data indicate that the recessive condition e′e′ was present in the exhibition line.

Intensity

Dryden (1921) used the two highest months in the yearly record as a measure of intensity and was able to make progress by selecting breeders on this basis. Hurst (1921, *loc. cit.*) employed the rate of laying as a percentage basis throughout the first year to measure intensity —30 per cent. being considered high. Goodale and Sanborn (1922) suggest as measures of intensity the months, the initial cycle, the inter-broody periods and the spring period. Harris and Goodale (1922) used the monthly basis as a measure of intensity as has been done by others. Hays and Sanborn (1927a) studied four possible measures and decided that mean winter clutch size is the most dependable.

Concerning the mode of inheritance of intensity, Hurst (1921, *loc. cit.*) reports that high winter intensity and high spring intensity each depend upon distinct dominant genes (W. S.). He believes that high autumn intensity depends upon a recessive (m).

Hays and Sanborn (1927a, *loc. cit.*) state that a mean winter clutch size of three or more eggs depends upon the presence of two dominant genes I and I′, that a clutch size of more than two but less than three depends upon gene I and that a clutch size of two or less indicates that both genes I and I′ are absent.

In these studies the females are grouped into three phenotypes with respect to winter clutch size, namely, II′, Ii′, and ii for clutch averages of 3 +, 2.1 to 2.9 and 2 –, respectively.

P_1 hens were all II′ in that their clutch size was three or more and, mated to an exhibition male, gave 27 II′, 18

TABLE 2

INTENSITY

Exhibition Sire J 711 (iiI′i′)	Production Dams (All Intense) J 1683 (IiI′i′)	J 2247 (IiI′i′)	J 2662 (IiI′i′)	J 2666 (IiI′i′)
	F_1 Daughters			
	27 II′ 18 Ii′ 9 ii′			
	F_2 Daughters			
5 II′ 16 Ii′ 20 ii′	1 II′ 3 Ii′ 6 ii′			

Ii′, and 9 ii′ daughters in F_1. This ratio shows that the male lacked one dominant gene for high intensity and that the females were not homozygous for both genes.

Highly intense (II′) F_1 females mated to an F_1 male gave 5 II′, 16 Ii′ and 20 ii daughters, again indicating the low intensity from the grandsire.

Two low intensity F_1 hens mated to an F_1 male gave 1 II′, 3 Ii′ and 6 ii′ daughters in F_2.

WINTER PAUSE

The cessation of production before March first of the pullet year has been called winter pause by Goodale and Sanborn (1922, *loc. cit.*). Hays (1924, *loc. cit.*) pointed out that winter pause behaves as a simple dominant in inheritance. Hays and Sanborn (1926) arbitrarily adopted a four-day cessation of production before March as indicating pause. Hays and Sanborn (1927, *loc. cit.*) showed that the duration of winter pause produced a very significant reduction in annual egg yield.

Birds pausing for four or more days are designated M while those lacking such a pause are m.

Three P_1 dams lacking pause (mm) mated to an exhibition male gave F_1 daughters, 25 non-pause to 11 pause.

One P_1 dam with pause gave 9 m to 9 M daughters.

TABLE 3

WINTER PAUSE

Exhibition Sire J 711 (Mm)	Production Dams* = Pause			
	J 1683 (mm)	J 2247* (Mm)	J 2662 (mm)	J 2666 (mm)
	F_1 Daughters			
	25 Non-pause	9 Non-pause		
	11 Pause	9 Pause		
	F_2 Daughters			
	19 Non-pause	3 Non-pause		
	19 Pause	10 Pause		

Mating four non-pause F_1 females to an F_1 male gave 19 m to 19 M F_2 daughters.

Mating two pause F_1 females to an F_1 male gave 3 non-pause to 10 pause F_2 daughters.

These data clearly indicate an inherited tendency to pause.

BROODINESS

Bateson (1902) and Hurst (1905) present data on crosses between broody and non-broody races indicating the dominant nature of the broody instinct. Hurst (1913) reports that broodiness behaves as a simple dominant. Goodale, Sanborn and White (1920) suggested that three genes might be concerned in the inheritance of broodiness. Punnett and Bailey (1920) partially confirmed Goodale's observations. Hays (1924, *loc. cit.*) confirmed the observation of Goodale that broodiness depends in its inheritance upon two dominant genes A and C, but was unable to discover a dominant inhibitor N.

Hays and Sanborn (1926a) showed that broody birds lay significantly fewer eggs than do non-broody birds. Hays and Sanborn (1927, *loc. cit.*) presented further conclusive evidence on the effect of duration of broodiness on egg yield.

Females are roughly designated AC if they go broody and ac if non-broody in the pullet year.

TABLE 4

BROODINESS

Exhibition Sire J 711 (AaCc)	Production Dams* = Broody J 1683 (Aacc)	J 2247* (AaCc)	J 2666* (AaCC)
	F_1 Daughters		
	6 Non-broody	10 Non-broody	
	2 Broody	19 Broody	
	F_2 Daughters		

One non-broody P_1 hen was mated to an exhibition male giving 6 non-broody and 2 broody F_1 daughters.

Two broody P_1 hens mated to the above male gave 10 non-broody to 19 broody F_1 daughters.

These data suggest that at least one of the broody genes was carried by the exhibition male. The F_2 daughters are now in their first laying year.

PERSISTENCY

Persistency followed by late molting at the end of the pullet laying year has long been recognized as a desirable characteristic associated with high egg records. Rice (1915, *loc. cit.*) stressed the importance of high persistency. Harris, *et al.* (1917, 1918, 1921, 1922), showed an important relation between fall laying and annual record. Goodale and Sanborn (1922, *loc. cit.*) consider persistency as a major, desirable characteristic. Hays and Sanborn (1927, *loc. cit.*) showed that persistency is the most important of the five traits considered in relation to egg records.

Hurst (1921, *loc. cit.*) states that high persistency is inherited as a simple Mendelian recessive. Hays (1927, *loc. cit.*) found high persistency to be transmitted as a simple dominant in Rhode Island Reds.

Birds laying for 315 days or more are persistent.

Three P_1 females, all high in persistency, were mated to an exhibition male.

TABLE 5

PERSISTENCY

Exhibition Sire J 711 (pp)	Production Dams (All Persistent) J 1683 (Pp)	J 2247 (Pp)	J 2666 (Pp)
	F_1 Daughters		
	14 Persistent 23 Non-persistent		
	F_2 Daughters		

The F_1 daughters showed 14 persistent to 23 non-persistent. This is an excess of non-persistent birds over the expectation of equality. No explanation is offered until further data are studied. Records on F_2 daughters are not yet complete.

ANNUAL PRODUCTION

The three P_1 production-bred females with complete records had annual egg records as follows: 261, 224, 224. These, when mated to an exhibition male, gave a total of 37 F_1 daughters. These F_1 daughters from the three dams gave the following mean records: 175, 190 and 209. The outstanding trait accountable for the superior record of the last family of daughters was persistency.

EGG SIZE

The mean egg size of most of the birds was recorded. Each egg was weighed during the period from February 22 to March 15, inclusive. Data reported (Hays, 1930) and other data on the flock indicate that first year maximum egg size appears either in February or March for the flock as a whole. This fact would suggest that maximum egg weight is reached in the pullet year at about ten months of age, which probably indicates, according to Waters' (1931) studies, that mature body weight is attained at the same time.

Birds may be arbitrarily classed as large-egg individuals if their eggs average 56.7 grams or more in Febru-

ary and March. Small-egg birds would lay eggs below this weight.

Of the four production-bred P_1 females, three laid large eggs and one laid small eggs. The F_1 generation of daughters showed 21 large to 12 small. The F_2 daughters were 18 large to 8 small. Egg size is superior in the exhibition strain and the F_2 generation shows a higher proportion of large-egg birds than the F_1.

TABLE 6

GENOTYPES

P_1 Sire
J 711—Eee′e′iiI′i′MmAaCcpp
P_1 Dams
J 1683—EoE′e′IiI′i′mmAaccPp
J 2247—EoE′e′IiI′i′MaAaCcPp
J 2662—Eoe′e′IiI′i′mm - - - - - -
J 2666—EoE$_1$e′IiI′i′mmAaCCPp

SUMMARY

In general, these data indicate that early sexual maturity behaves as a dominant in crosses between early-maturing production-bred and late-maturing exhibition-bred Rhode Island Reds. High intensity behaves in the same general way as early sexual maturity. Winter pause behaves as a dominant trait. Broodiness was increased by crossing, probably due to the introduction of one of the essential complementary genes from each strain. There is an excess of non-persistent F_1 daughters over expectation on the basis of simple dominance. Annual egg records were smaller in F_1 daughters than in the production strain. Egg weight at mature body weight increased in F_2 over F_1.

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AN ALLEGED CASE OF INHERITANCE OF ACQUIRED CHARACTERS

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ON May 4, 1932, I received the following letter from the librarian of the City Library, Springfield, Massachusetts:

A young married woman on my staff, when about twelve years of age, sustained an injury to her hand by being hit with a croquet mallet, which resulted in the disappearance of the knuckle, a marked shortening of the finger, and a slight curvature of the finger. She tells me that her daughter, about ten years of age, shows an almost identical deformity. This would appear to be a case of the inheritance of an acquired character.

She wrote about the matter to a university professor in Texas, who replied that such a result was impossible. This seemed to be a strange attitude for a scientist. I have understood that rare cases of the apparent inheritance of an acquired character have been reported, and I should suppose that a scientist would be interested to verify the facts rather than to declare them impossible on general principles.

On May 14 the following letter was received from Mrs. Ernestine R. Fernald,* of the Springfield Library:

Mr. Wellman has asked me to reply to your letter of May 12, addressed to him, as I and my daughter are the subjects of the discussion in question, and perhaps can supply more complete information.

First, I will describe the finger as it is now—of necessity, in untechnical language. The knuckle bone, which ordinarily humps up in closing the fist, is gone entirely, and this is the most important bit of evidence I have to prove that my daughter has inherited a mutilation, as I will explain further on. The finger appears to be one-half inch shorter than the corresponding finger on the other hand but actually it is not, because the joint (where it joins the hand) is now about a half inch further into the hand (toward the wrist) than normal, leaving the actual finger-bone of normal length. [See Fig. 1.]

The accident occurred as follows: I reached for my croquet ball to pick it up and move it, and my friend at the same moment started to knock it over to me with her mallet. Her mallet came down with much force on that knuckle. Immediately after the accident the *knuckle-bone was there* and humped up as usual but pushed back from its usual position. This I know is positively true. I remember seeing it so clearly and after it was set that night (I took ether) there was much talk between the doctor and my mother over the fact that the little knuckle bone had dropped down in some

* Permission granted to print name.

place but that I was young enough so that it would undoubtedly be absorbed—as it has been.

My daughter's hand is identical with mine, as it is now. Not almost the same, but identical as far as can be observed from the outside. (See Fig. 1.)

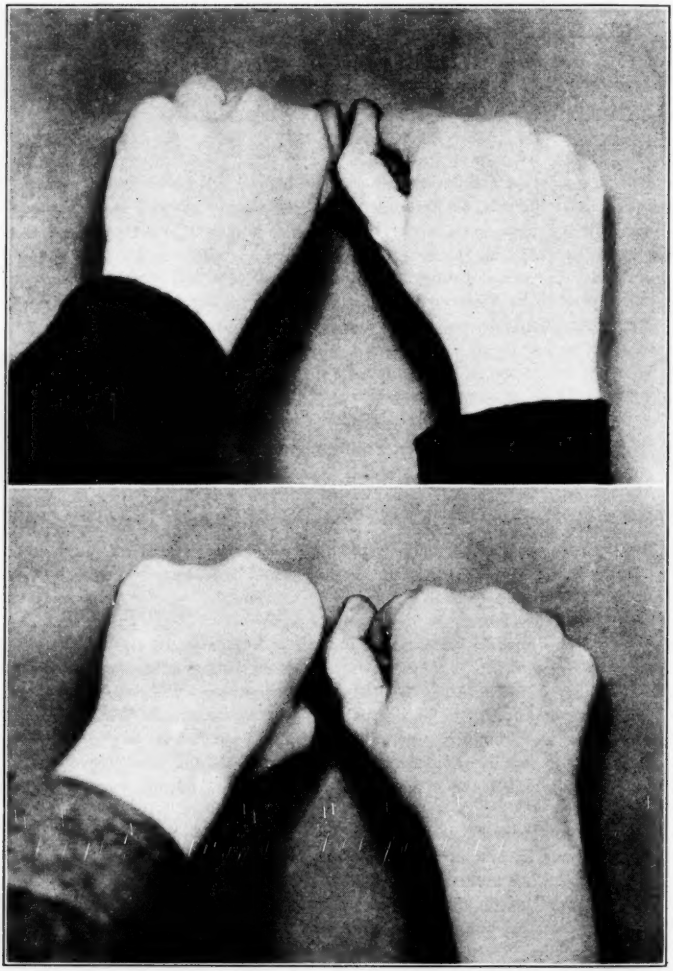

FIG. 1. Photograph of the hands of Mrs. Fernald, showing short fourth metacarpal on left hand (above); and of Elizabeth Fernald, showing short fourth metacarpal on left hand (below).

In view of the above facts, it would not matter much whether there was any malformation of that finger—and I am very sure there was not—before the accident or not, would it? At least it was definitely different after the accident, and my daughter's is exactly as mine is now.

Perhaps this is sufficient explanation for this letter. If you wish any more facts or details, I will be glad to supply them. My interest in the matter has been whetted by the many books I have read which say it can not happen, when I know it has happened!

X-rays of the hand of Mrs. Fernald and her daughter, Elizabeth, showed that in both cases the fourth metacarpal of the left hand was shorter than the other metacarpals, about 28 per cent. less than the average of the third and fifth metacarpals (Figs. 1–2). In the daughter of 10½ years the fourth metacarpal shows no such separate epiphysis as is found at the distal end of the second, third and fifth metacarpals. If a short epiphysis was ever formed it was of small size and fused early with the diathesis. In the mother the shaft of the bone is slenderer in all the metacarpals than in the daughter. The distal end of the fourth metacarpal is similarly molded to that of the daughter.

Mrs. Fernald having stated that she was interested in genealogy the suggestion was made to her to request all her relatives to send in outlines of their hands and feet, and similar outlines were obtained from Mrs. Fernald, Elizabeth Fernald and Mrs. Fernald's father.

Since Mrs. Fernald's mother is dead, it was impossible to make first-hand observations upon her hand. Her father's hand, however, showed no deformity; only a slight extension of the web between second and third toes. An examination of the contours of hand and feet sent in by Mrs. Fernald showed no other case of an especially short finger, although in five cases out of eighteen in the family the fourth digit is shorter than the second by a few (1 to 8) millimeters. The persons showing this near equality of the fourth and second digits are in two cases on Mrs. Fernald's father's side (first cousins of Mrs. Fernald) and in one case on her mother's side. No abnormalities of the toes of the feet were found in the

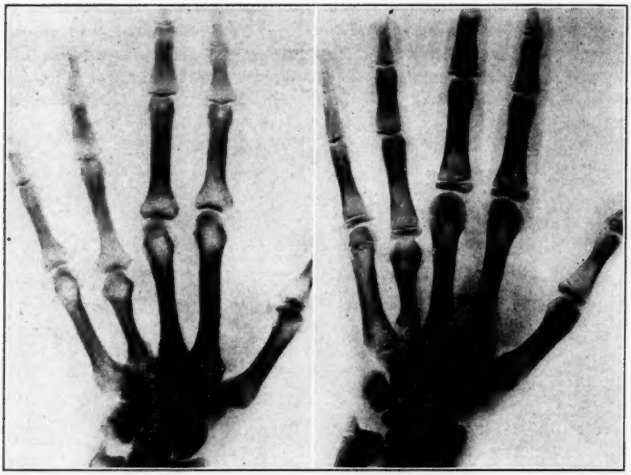

FIG. 2. Radiograph of left hand of Mrs. Fernald, showing short fourth metacarpal bone (left); and of left hand of Elizabeth Fernald, showing short fourth metacarpal bone (right).

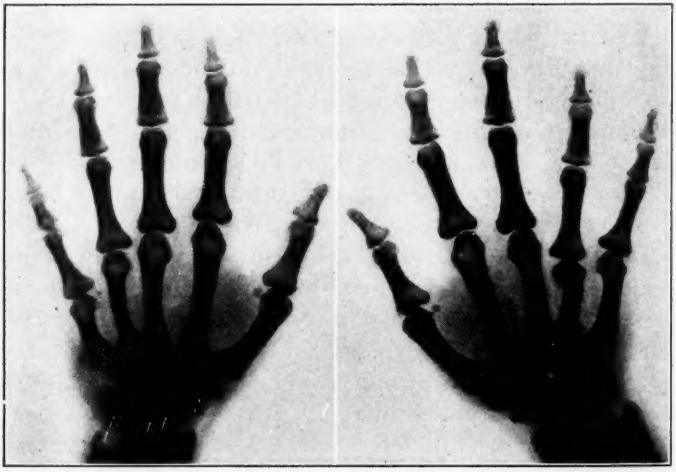

FIG. 3. Radiograph of hands of Ada B., showing short fourth metacarpal bone on right hand (a); the third and fifth metacarpals also reduced in length. On the left hand (b) the fifth metacarpal is greatly reduced in length, the third and fourth metacarpals slightly reduced.

propositus or collaterals. Correspondence brought out, however, two things: One, that a first cousin once removed of Mrs. Fernald stated that Mrs. Fernald's mother's father had short fingers perfectly formed. Also it was learned that a second cousin of Elizabeth Fernald by the name of Ada B. (III, 1), living in Detroit, had a short metacarpal on the right hand. X-rays were kindly furnished by this woman, and are shown in Fig. 3. These reveal a short fifth (also fourth) metacarpal on the left hand and a short fourth (also fifth) metacarpal on the right hand. This metacarpal of the right hand is very different in form from that of Mrs. Fernald, the axis being somewhat curved. Miss B.'s mother's fourth digit on left hand is 6 mm shorter than the second digit; while the two are equal on the right hand. Also, her right fifth finger is exceptionally short.

The pedigree chart of the family of the mother's side of Mrs. Fernald showing affected individuals is given in Fig. 4.

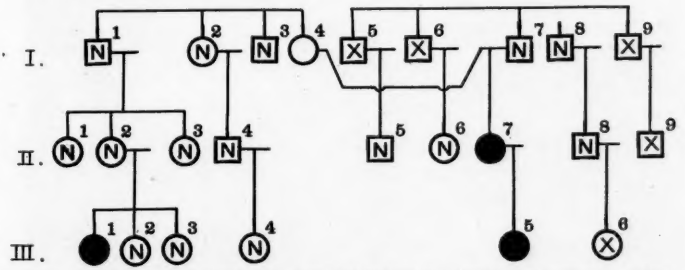

FIG. 4. Pedigree chart of Fernald-Morse-B. family. Squares, males; circles, females. Black symbols, persons with strikingly short metacarpals. N, hands that do not deviate strikingly from the average hand. X, no data. The father of generation I 1–4 (not charted) is said to have had short fingers, as did his brother and this brother's daughter. I 7 has a slight webbing, zygodactyly, between 2nd and 3rd toes, seen also in his daughter II 7 and her daughter III 5, also in his brother and another brother's son. Such a slight zygodactyly is found in a considerable fraction (say 5 per cent.) of the population. II 2 has on the left hand (only) a fourth digit that is 6 mm shorter than the second. On the right hand the fifth digit is exceptionally short. II 4 has a slight webbing between 2nd and 3rd toes on both feet. II 5 hands and feet of average form. III 4 has a slight zygodactyly between 2nd and 3rd toes of right foot (only).

An examination of the files of the Eugenics Record Office reveals a somewhat similar case in a young woman who furnished photographs, as shown in Fig. 5. In this

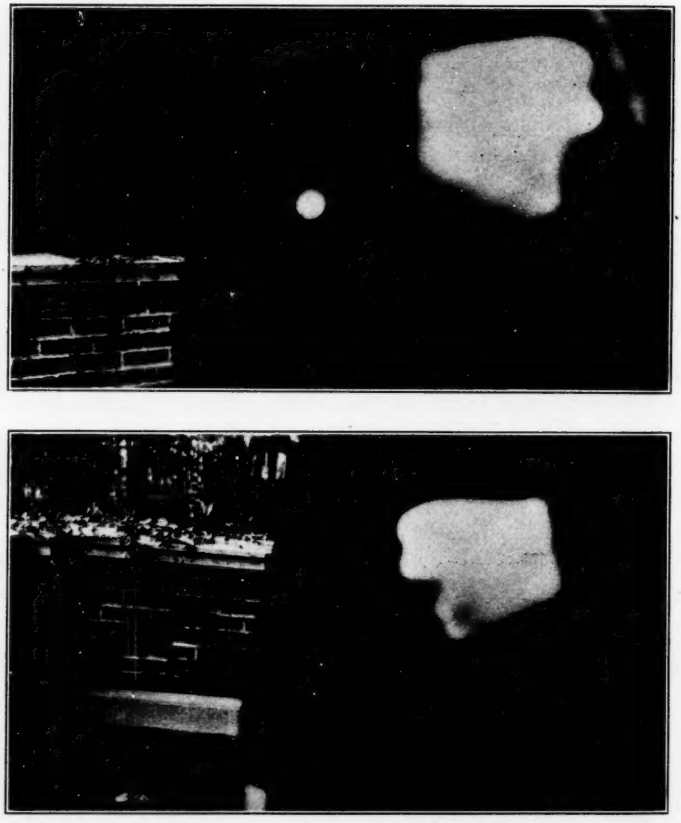

FIG. 5. Photograph of right (above) and left (below) hands of R. F. W. (ERO files; A: 2143–11, 12).

case there was a short metacarpal on both the right and left hand. Also the hand of the wife of one of the staff members of this department has a strikingly short fifth metacarpal.

Day (1915) has described and figured short fourth metacarpal bones in the right and left hands of a patient

in whom the fourth metatarsal bone was also short. A very similar defect has been described by Boorstein (1916) for the fourth metacarpal; and in another case a somewhat similar shortening of the fifth metacarpals. In Case I there was a similar defect shown in two sisters, an uncle, an aunt, grandmother of the patient and four other members of the family. In Case II, a girl of nineteen years, there was nobody in her family, so far as known, who had a similar deformity. Boorstein adds: "Her mother, in trying to explain the case of the defect, voluntarily offered the well-known explanation that it was due to some fundamental impression received by her during pregnancy (telegony[1])."

Variation in the length of the metacarpal bones has been repeatedly described; the development of radiography has called attention to scores of such cases.

The commonest type is that shown in the Fernald family. The cases of Day (1915), Miskolczy (1929[a]) and Lewin (1917) show a close similarity to the Fernald case. Other cases are cited by Fontana and Vacchelli (1902), Hochheim (1904), Kenyeres (1905), Machol (1907), Mathew (1908), Chevallier (1919), Miskolczy (1929[b]).

In other cases two or more metacarpals are involved in the shortening, as in Fig. 6 from Boorstein (1926). Mosenthal (1911) has described shortened 4th and 5th metacarpals, Friedländer (1916) short 3rd and 4th and 2nd and 5th metacarpals, and Miskolczy (1929[a]) 3rd and 5th metacarpals.

Since Machol (1907), Chevallier (1919) and Pol (1920) have published good bibliographies and as later works are cited in Index Medicus, a complete bibliography is not needed here.

Deviations from typical development of the hand and feet are wide-spread. Brachymetacarpaly is only one type. Brachyphalangy, fusion of phalanges, curvature

[1] What is meant is "maternal impression." Telegony refers to the influence of the first sire upon the quality of subsequent offspring.

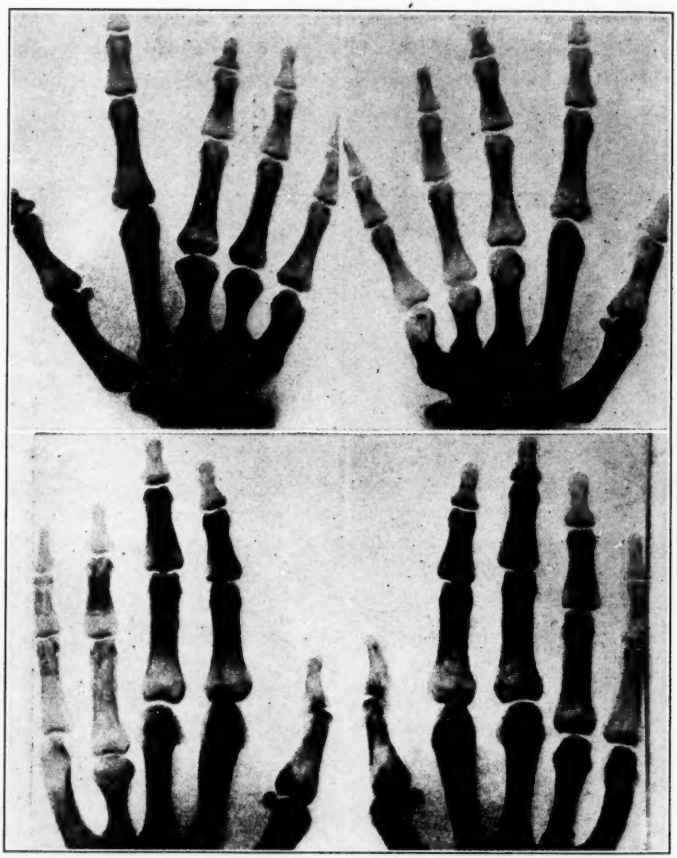

FIG. 6. *Upper:* Roentgenogram of two hands of girl 15 years of age, showing 3rd, 4th and 5th metacarpals of both hands to be short. *Lower:* Roentgenogram showing right and left hands of the father of girl in Fig. 6. The fourth fingers are short, the one on the right hand being the longer. The roentgenogram showed that the fourth metacarpal of the left hand was exactly the same shape as that of the daughter. (S. W. Boorstein, *Surgery, Gynecology and Obstetrics,* November, 1926, pp. 654–658.)

of fingers, especially of the fifth, zygodactyly, syndactyly, have been repeatedly described not only in humans but also in mice, guinea-pigs and poultry. Some of these digital defects, and others, will doubtless appear in other

animals, as more species are bred in captivity and carefully examined.

Indeed, it is remarkable that so often just five digits should appear out of the embryonic paddle, that they should be so nearly of the same relative length and should have so nearly the same bones in number and proportionate lengths. There are evidently many genes that direct the shaping of the hands and feet and if one of these is missing or modified the distal end of the appendage is modified also.

To sum up, it appears that in the Morse-Bedell branch of Mrs. Fernald's family there is a tendency toward abnormally short metacarpals; that she, as well as her daughter, inherited this tendency; that the accident which injured the fourth knuckle in Mrs. Fernald's 12th year first called attention to the short metacarpal. It is probable, however, that the short metacarpal existed before the accident. It is noteworthy, Mrs. Fernald informed me, that she noticed the short metacarpal in her daughter Elizabeth only when she had acquired the age of eight years. The hand of children is often pudgy, so that abnormalities in the growth of the metacarpals would not be readily noticed.

The case is of interest as throwing light upon the development of the idea of acquired characters. An accident calls attention, for the first time, to a defect. The defect is ascribed to the accident. Subsequently, the affected individual has a child with the same defect and this defect is ascribed to the accident that happened to the mother. The chain of evidence seems to the casual observer complete. The one fact that is missing is that the first observed defect is antecedent to the accident.

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SHORTER ARTICLES AND DISCUSSION

TWO NEW ALLELOMORPHS FOR HETEROSTYLISM IN PRIMULA

ERNST (1928) analyzed the inheritance of heterostylism in *Primula hortensis* and *P. viscosa,* of the *Auricula* group. He postulated two closely linked genes, one affecting style length, the other anther height. Brieger (1930) and Stern (1930) interpreted his results on the basis of four allelomorphic genes. Recently Ernst (1933) has published results which show the existence of six allelomorphs at this locus. The new genes differ from the old as regards their effect on the pollen grains. So far all normal thrum (short-styled, high-anthered) plants have large pollen, and all normal pin (long-styled, short-anthered) have small pollen. But each of the intermediate or homostyle types may have large or small pollen. In *viscosa* only a minority of homostyle thrum (short style, low anther) plants have large pollen, but the group of characters is inherited as a whole. Similarly, when the long-styled, high-anthered form of *hortensis* is crossed with *viscosa,* the pollen-grains associated with this type of flower are always small in later generations. The various phenotypes are given in Table I. In devising symbols for the allelomorphs the first index refers to the style, the second to the anthers, the third to the pollen. The dominant gene of normal thrums is denoted by S instead of s^{+++}, and the recessive of normal pins by s instead of s^{---}. Of the eight possible genes s^{++-} and s^{--+} have not yet been described. Dominance is always complete, as regards the $^+$ characters. The various genotypes actually found in Ernst's material are given in Table I. Others are possible. For example, $s^{+--}s^{-++}$ should give normal thrum plants.

Two other characters were determined by this group of genes, namely, length of stigmatic papillae and fertility on crossing. The long-styled plants generally have longer papillae. One long-styled high-anthered plant had medium length papillae, but its genetics were not investigated. The relative sterility of "illegitimate" unions varies in different cases, but it is not clear whether this is due to genetical causes. Nevertheless, multiple allelomorphism as regards these characters is not impossible.

TABLE I

Species	Style	Anthers	Pollen	Genotypes
hortensis and viscosa	short	high	large	S–, $s^{+-}s^{-+}$, $s^{+-}s^{+-}$
viscosa	short	low	large	$s^{+-}s^{+-}$, $s^{+-}s$
viscosa	short	low	small	$s^{+-}s$
viscosa	long	high	large	$s^{-+}s^{-+}$, $s^{-+}s$
hortensis	long	high	small	$s^{-+}s^{-+}$, $s^{-+}s$
hortensis and viscosa	long	low	small	ss

We have here another case in which the natural polymorphism of a species is due to a series of allelomorphs or very closely linked genes. Such are the allelomorphs determining self- and cross-sterility in many plants, the autosomal allelomorphs for color in *Cepea, Paratettix,* etc., and for blood groups in *Homo,* and the sex-linked allelomorphs for color in several fish species and the beetle *Phytodecta.* On the other hand, the natural trimorphic heterostylism of *Lythrum salicaria* and *Oxalis floribunda* is due to genes in different chromosomes, as is the tetramorphic heterostylism of the cultivated *Primula sinensis.*

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HYBRID MUTATIONS

INVESTIGATORS have often pointed out that gene mutations sometimes occur following hybridization. This seems very probable *a priori* but it is rather difficult to demonstrate experimentally. The hybrid embryo produced after interspecific crosses is,

in a sense, something more or less foreign for the maternal organism and in the F_1 hybrids the maternal contribution may be considered as being in some respects foreign for the paternal one and *vice versa*. According to the degree in which these contributions are foreign they may act very much like certain well known agents which increase the mutation rate. It is rather difficult, however, to separate the mutations induced by hybridization from the combinations also possible in the F_2-generation.

Recently I observed a number of instances indicating hybrid mutations which seem worth reporting. These instances fall into two groups; in the first group are the plants appearing in the F_2 which are considered mutations because they carry homozygous recessive genes while the parents had homozygous dominant allelomorphs; in the second group are polymorphic trigenomal species hybrids of *Nicotiana* which originated from homozygous pure species.

First Group: Appearance of plants in the F_2-generation carrying recessive genes in a homozygous condition while the parental plants both had dominant allelomorphs in a homozygous condition. Two instances fall into this group.

(a) A cross of very distantly related varieties of homozygous red pepper (*dolma* and *kamby*) gave 1.37 per cent. offspring in the F_2-generation that had orange peppers when ripe.

(b) Two hybrids of *Secale cereale* and *Secale montanum*, homozygous for the presence of normal chlorophyll, gave a few chlorophyll albinos in the F_2-generations. One hybrid gave 6.6 per cent. and the other gave 25.0 per cent. of these mutations, while four other sister F_1 hybrids gave only normal green progeny.

Second Group: Appearance of polymorphic trigenomal species hybrids in *Nicotiana* produced from combinations of homozygous pure species. Under this type I shall give only a few of numerous instances.

(a) Seeds were obtained from the F_1 of *Nicotiana glauca* (n–12) × *N. Langsdorffii* (n–9) when crossed back with *N. Langsdorffii* and 35 plants were raised. Of this number 30 were studied cytologically and all found to have 30 somatic chromosomes, *i.e.*, 12 from *glauca*, 9 from *Langsdorffii* of the first crossing, and 9 from *Langsdorffii* of the back crossing. In *Nicotiana* the first

meiotic division is the reduction division. This first division may occasionally fail to occur in the hybrid *glauca* × *Langsdorffii* so that at the end of the first meiotic division nuclei are formed which have 21 chromosomes, the diploid number of the hybrid. During the second division these chromosomes divide longitudinally and gametes are formed with 21 chromosomes; when such gametes are fertilized with gametes of *Langsdorffii* trigenomal plants originate. Theoretically such plants should be uniform, like the F_1 hybrids, for the component species are homozygous and each of the trigenomal plants has one genom of *glauca* and two genoms of *Langsdorffii*. However, 9 of the trigenomal plants differed morphologically from the other 21 plants which were uniform. These 9 plants differed in the shape of their leaves, the size and shape of the flowers, the length of the styles, etc. Such differences may be due to chromosome translocations, inversions, etc.; or to gene mutations. No indications were found in the somatic chromosome behavior to suggest chromosomal abnormalities. In order to separate the first types from the second the gametogenesis of these trigenomal hybrids was studied, since it is known that chromosome translocations and inversions usually lead to marked abnormalities in the reduction division. Of the 21 monomorphous trigenomal hybrids, 3 showed marked disturbances in the gametogenesis. Similar disturbances were found in 4 of the 9 polymorphic plants. The other 5 of the polymorphic plants showed gametogenesis to be similar to that observed in the other 18 monomorphous plants. These 5 plants were suspected to be hybrid mutations.

(b) The trigenomal triple hybrids produced by crossing the hybrid *N. Tabacum* (n–24) × *N. tomentosa* (n–12) with *N. Rusbyi* (n–12) have one genom of each of the component species, *i.e.*, 48 somatic chromosomes. Therefore, theoretically, these plants should be uniform since the parental species were homozygous. Actually, however, two of these trigenomal plants differed in the manner already described in the preceding case.

(c) The triple, fully fertile hybrids of *N. Tabacum* × (*N. sylvestris* × *N. Rusbyi*) produced recently from homozygous pure species at a temperature about 20° C. have one *Tabacum* genom (n–24), one *sylvestris* genom (n–12), and one *Rusbyi* genom (n–12), *i.e.*, 48 somatic chromosomes. In these plants gametogenesis is regular and they should be identical, but actually the plants differed in many ways: size and shape of the leaves, color of the flowers, length of the styles and anthers, size of the whole plants, maturation period, etc.

(d) Some of the trigenomal hybrids of (*N. Tabacum* × *N. tomentosa*) × *N. tomentosa* also produced from homozygous species differed markedly morphologically, although their gametogenesis was like that of the uniform trigenomal hybrids. Similar cases were also observed in other trigenomal hybrids but these and detailed data will be published elsewhere.

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OMPAX SPATULOIDES CASTELNAU, A MYTHICAL AUSTRALIAN FISH[1]

O flesh, flesh, how art thou fishified!
—*Romeo and Juliet.*

SYSTEMATIC ichthyologists usually encounter sufficient difficulties in identifying natural species without having fraudulently "manufactured" fishes brought before their notice by practical jokers. In the past, several zoologists have soberly considered as actual fishes specimens, or, more often, accounts or illustrations of such, which have later proved to be mere fakes, some of which have even been given scientific names, though these, of course, have no status in modern nomenclature.

A classic instance is that of the erratic genius, Rafinesque, who was at one time the guest of Audubon at Hendersonville, Kentucky. Rafinesque tried to catch bats by beating them down with Audubon's violin, quite wrecking the instrument in his

[1] By permission of the Trustees of the Australian Museum.

enthusiasm to procure specimens. For revenge, Audubon prepared paintings of some entirely imagined fishes, which Rafinesque described as new genera and species in his "Ichthyologia Ohiensis," 1820.

Again, the generic names *Uriphaeton* Swainson 1839 (*Urophaeton* Agassiz 1846) and *Phaetonichthys* Bleeker 1876 are based on *Serranus phaeton* Cuvier and Valenciennes (Hist. Nat. Poiss, ii, Oct. 1828, p. 309, pl. xxxiv), a "species" described from a fallacious specimen in which the head of a grouper (*Cephalopholis*) has had the tail of a "flute-mouth" (*Fistularia*) attached to it.

Mermaids, Jenny Hanivers, three-eyed haddocks and faked photographs of giant fishes, trout leaping waterfalls, etc., are other traps for the unwary. These are, of course, distinct from teratological specimens, the fabulous fishes of mythology, heraldry and ancient religions, some sea-serpents, and the abstract creations of mendacious anglers, concerning all of which there is a considerable literature.

Many years ago, in the Proceedings of the Linnean Society of New South Wales (iii, 1879, p. 164, pl. xix*a*), Count F. de Castelnau wrote a short paper "On a New Ganoïd Fish from Queensland," as follows:

> I have received from Mr. Staiger of the Brisbane Museum a drawing of a very remarkable fish, with the following note: "It is only found in a single water hole in the Burnett River, living together with *Ceratodus;* and when, in August 1872, I was in Gayndah, I got it on the breakfast table, brought in by blacks from a distance of about eight to ten miles. I had the fish for breakfast, remarked its curious shape, and asked the then Road Inspector to draw it for me, which he did. *Ceratodus,* not well known then, formed the dinner. I was not connected with any scientific body, otherwise I would have, at any rate, preserved the head. The person who drew it is not an ichthyologist but still is a draughtsman."
>
> On examining the rough and incomplete sketch, I saw immediately that the fish was a *ganoïd* nearly allied to *Atractosteus,* but forming, by its dorsal, caudal and anal fins, all united, the type of a new genus, and probably of a new family.
>
> It is remarkable that all the species of *ganoïd* fishes known, having a long, more or less, crocodile back, are until now, only from America. It is evident that from such a drawing no correct description can be given; all I can say is that it shows the existence in Australia of a *ganoïd* fish with a very elongate and very depressed spatuli-form snout; this is much narrower at its base than towards the two-thirds of its length; it is rounded and bordered at its extremity, having very much

the form of the beak of the *Platypus*, the two jaws are of about equal length; the eye very small and placed near the upper part of the head; the body is covered with large *ganoïd* scales; the pectorals appear small, and are placed immediately behind and below the head; the vertical fins are very long and united, but notwithstanding, the caudal seems rather distinct; nothing is said of the dentition. Mr. Staiger says also that the fish is of a dirty mahogany color; and he adds that "*the first of the four rays is very strong*"; but I cannot find out to what this applies. The specimen was about eighteen inches long. As I have already said, the fish that comes the nearest to it is the *Atractosteus spatula* of Lacepede; much better figured by Aug. Dumins [= Duméril—G. P. W.] in his *Histoire Naturelle des Poissons*, vol. II, p. 361, pl. 24, fig. 7.

In our present knowledge of this singular fish, some inconvenience might arise from giving it a significant name; and I think it is preferable to design it under the mysterious historical one of *Ompax*. The species will bear the name of *spatuloïdes*.

It is much to be desired that some specimens will soon be found and secured for one of the Australian Museums.

Ompax, by its extraordinary snout, comes also near *Polyodon*, of which one species is found in the Mississippi, and another in the great Chinese river, the Yantsekiang; but these have their body naked, and cannot properly be placed with the *ganoïds*.

It is singular, but almost certain, that the teeth of *Polyodon* fall before the fish acquires its full size.

Castelnau's paper naturally came in for a certain amount of criticism. The Zoological Recorder, O'Shaughnessy (*Zool. Record*, xvi, 1879 (1881), Pisces p. 5) opened with a broadside:

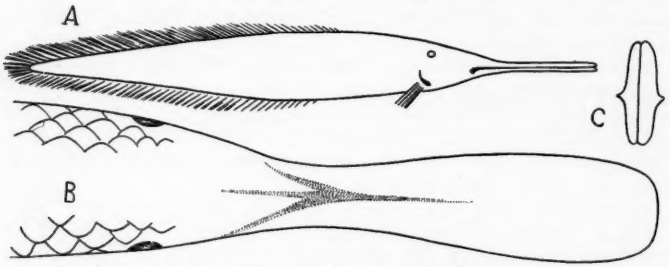
. . . Castelnau founds a new genus, and probably a new family, on a specimen of Ganoïd fish allied to *Atractosteus which had been eaten for breakfast by a Mr. Staiger, and all the characters of which are gathered from a drawing made after and not before the repast.* He designates it "in the present state of our knowledge of this fish, by the mysterious historical name of *Ompax.*" In the present state of our knowledge, the Recorder thinks he would be scarcely justified in admitting *Ompax spatuloides*, sp. n., into the system.

Sir William Macleay (Proc. Linn. Soc. N. S. Wales vi, 1881, p. 348, and Descr. Cat. Austr. Fish. ii, 1881, p. 284) remarked upon the species as follows:

1069. OMPAX SPATULOIDES, Castelnau.

The description of this genus and species will be found, with all the details known or remembered, in the Proceedings of the Linnean Society of New South Wales, Vol. III., p. 164, pl. 19 A., figs. 1–2–3. I think it is probable that no such Fish was ever found, but I give it a place in my Catalogue, in order to direct attention to the subject, as the liklihood [*sic*] of finding Ganoïd Fishes in Queensland waters is asserted by several very distinguished Naturalists.

Ompax spatuloides has perforce been retained in lists of Australian or Queensland fishes, and figures in the most modern Check-List (McCulloch, Austr. Mus. Mem. v, 1929, p. 33), and the generic name, which Rye (Zool. Record xvi, 1879 (1881), Index new gen. p. 8) had regarded as preoccupied by *Omphax* Guénée 1857, Insecta, was included in Jordan's "Genera of Fishes" and classified with the Ceratodontidae (Genera of Fishes iii, 1919, p. 399, and Classif. Fish. 1923, p. 110).



A. Castelnau's *Ompax spatuloides* shown in lateral view.
B. Head and snout of the reputed fish seen from above.
C. Cross-section through the snout of *Ompax*.

Some months ago, my colleague, Mr. J. R. Kinghorn, of the Australian Museum, drew my attention to an article in the well-known Sydney paper, *The Bulletin* (Aug. 6, 1930, p. 21), in which the mystery of the identity of *Ompax* is solved by an author using the pseudonym "Waranbini." His account is as follows:

A sweet-scented gum (*E. staigeriana*) of the northern parts of Queensland perpetuates the memory of Carl Theodore Staiger, who was at one time director of Brisbane Museum, and was made the victim of one of the quaintest jokes in scientific history. While he was visiting Gayndah station the hard-cases there prepared a new fish for Staiger, made of the head of a lung fish, the body of a mullet and the tail of an eel. It was nicely cooked and placed before him for his breakfast, with the remark that it was something new—a very rare fish that had never been seen anywhere but at Gayndah. Mr. Staiger was immensely interested, and expressed regret that he had not seen it alive. On being told that it might be months before another was caught, he made a careful sketch of the cooked specimen before he started to eat it. The sketch and a description were subsequently sent to an ichthyological expert, Count Castelnau, and that gentleman named it *Ompax spatuloides*. Whenever a marine [!] mystery was captured afterwards in the Gayndah district, the locals would remark with a grin that it "must be an Ompax!"

From this account, it is obvious that *Ompax spatuloides* is a purely mythical genus and species, whose disgraced name must be removed from the Australian list.

The account given by "Waranbini" contains one or two minor discrepancies when compared with Castelnau's but these may be due to a lapse of memory which is pardonable when it is recalled that half a century had passed between the times of appearance of the two. In the modern account, for instance, the head of a lung fish is said to have been used in the preparation of *Ompax*, but to the present writer it seems more likely that the head of some fresh-water Long Tom (family *Belonidae*), or perhaps even a Platypus bill, may have been utilized in this strange concoction.

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THE EFFECTS OF ALPHA-RADIATION FROM POLONIUM ON THE DEVELOPING EGGS OF *DROSOPHILA MELANOGASTER*[1]

WHILE the biological effects of radiation from other members of the radium family have been studied widely in recent years, alpha-radiation from polonium is still the object of relatively rare investigation.

Lacassagne and his associates[2] (Fondation Curie, Institut du Radium, Paris), studying the effects of polonium solutions injected into the organism, have observed (1924–1928) profound changes in the blood and histological changes in certain organs, particularly glandular tissues and organs of excretion: the kid-

[1] The expenses of this investigation were supported in part by a grant from the committee on the effects of radiation upon living organisms of the National Research Council.

[2] A. Lacassagne and J. Lavedan, "Les Modifications Histologiques du Sang Consécutives aux Irradiations Experimentales." *Paris Médical*, 51: p. 97, 1924; *ibid.*, "Modifications Numériques des Elements du Sang Sous l'Influence des Irradiations Experimentales." *La Médecine*, Nc. 9, June, 1924; A. Lacassagne, J. Lattés and J. Lavedan, "Etude Experimentale des Effets Biologiques du Polonium Introduit dans l'Organisme." *Jour. de Rad. et d'Elect.*, 9: 1–82, 1925; A. Lacassagne, "Modifications du Sang Determinées par les Rayons-X et les Corps Radio-actifs." *Progrès Médicale*, 30: 1077–1087, 1928.

ney, the skin, the thymus, the genital and adrenal glands, the liver and also the lungs. Emile-Weil and Lacassagne[3] (1925) recorded the production of grave anaemia and leucemia due to numerical modifications of the blood-elements and because of injuries to the blood-forming tissues.

In investigation of the action of radium salts on colloids, Hardy[4] incidentally discovered the effects of alpha-radiation alone upon globulin solutions, rendered acid or alkaline by the addition of dilute acetic acid or ammonia. When the solutions exposed to 50 mgms. of radium bromide were separated from the radiation source by two thin layers of mica of the containing capsule (which would shut out all alpha-rays), no changes were perceptible even after one hour's exposure. When, however, samples of the globulin solutions were exposed as naked hanging drops, changes were apparent at the end of three minutes' time. The acid solution became clearer, showing thereby more complete solution. The alkaline solution turned to an opaque jelly. The physico-chemical explanation of this phenomenon is interesting in itself, but from the biological point of view such a result may be considered important as showing that exposure to alpha-radiation produces effects which differ both in kind and in degree from those caused by exposure to the beta and gamma-rays.

Lacassagne and Desclin[5] (1928) exposed the eggs and young embryos of frogs to alpha-radiation from polonium. They obtained destruction of localized areas with minimum traumatism. While entodermal invagination was perfectly normal, as development proceeded, these localized areas produced malformations of specific organs or regions, especially the olfactory organ, the optic and auditory vesicles, the cervical and branchial regions.

Swann and del Rosario[6] (1931), in studies upon the effects of radioactive substances upon Euglena, have found that alpha-particles kill the animals in proportion to the strength of the

[3] P. Emile-Weil and A. Lacassagne, "Anémie Pernicieuse et Leucémie Myéloide Mortelles Provoquées par la Manipulation de Substances Radioactives," *Bull. de l'Acad. de Méd.*, 93: No. 9, 1925.

[4] W. B. Hardy, "The Action of Salts of Radium upon Globulins," *Proc. Physiol. Soc.*, May 6, 1903: 29–30.

[5] A. Lacassagne and L. Desclin, "Sur l'Emploi des Rayons-Alpha du Polonium en Embryologie, comme Agents de Destructions Localisées." *Compt. Rend. Soc. de Biol.*, 99: p. 98, 1928.

[6] W. F. G. Swann and C. del Rosario, "The Effect of Radioactive Radiations upon Euglena." *Jour. Franklin Inst.*, 211: 303–317, 1931.

dissolved emanation present in the water. Rona (Institut für Radiumforschung, Vienna) finds that the spores of the mushroom, Mucor, are killed by five minutes' exposure to polonium (unpublished results). Other research workers associated with her (Blau, 1931[7]; Blau and Kara-Michailova, 1931[8]) have studied physical aspects of the radiation from polonium.

The present authors are investigating the effects of alpha-radiation from polonium upon Drosophila eggs (wild-type flies) in different stages of their development. During preliminary experiments to determine the dosage in exposure time the spores of two species of mould were irradiated. Fifteen minutes' exposure killed the spores so that no cultures developed. Cultures already growing were prevented from fruiting and soon died out.

The polonium used was radium F, a substance which gives off practically only alpha-rays. It is the last radioactive element of the long radium family, its products of disintegration being helium and lead. The mean life of solutions of this polonium is 196 days. From a suitable solution the polonium is deposited on a silver disk. This in turn is attached to a silver plunger, and the whole is enclosed in a small brass cylinder, which is mounted with adjustable screws. Eggs and spores were treated in petri dishes on an agar medium. The adjustable brass cylinder and the plunger arrangement enable the disk to be brought into close proximity with the surface of the culture medium. Radiation effects upon eggs in two stages of development have been studied especially: (a) collected within a quarter of an hour after laying from a large number of females of the same age—eggs fertilized, divisions just beginning—*preblastula stage;* (b) collected two and one half hours after laying —blastula complete, polar cells aggregated—*blastula stage.* These stages were identified in time from cytological studies made previously in connection with other experiments, which accord almost exactly with those recorded by Geigy (1931[9]) in

[7] Marietta Blau, "Über das Abklingen des latenten Bildes bei Exposition mit Alpha-Partikeln." *Sitzungs. der Akad. der Wissenschaft.* Wien, 140: 623–628, 1931.

[8] Marietta Blau and E. Kara-Michailova, "Über die durchdringende Strahlen des Poloniums." *Sitzungs. der Akad. der Wissenschaft.* Wien, 140: 615–622, 1931.

[9] Rodolphe Geigy, "Action de l'Ultra-violet sur le Pôle Germinal dans l'Oeuf de Drosophila Melanogaster." Genève, Albert Kundig, 1931.

his investigations of the action of ultra-violet light on the germinal pole of Drosophila eggs. The individual differences in eggs collected in this way are not great.

Eggs were exposed in the pre-blastula and the blastula stages to irradiation of five and fifteen minutes' duration. The experimental results given briefly in the following table indicate a higher sensitivity in the blastula stage as shown by the greater percentage of eggs failing to hatch. In each instance where irradiation was made in the blastula stage, all the larvae hatching from irradiated eggs died within three hours after hatching. Where irradiation was made of eggs in the pre-blastula stage, all the larvae hatching survived to pupate and become adult flies.

No. eggs	Stage	Exposure time	Electrostatic units	Per cent. of eggs hatching	Remarks
100	pre-bl.	5 min.	2,604	56	living flies
100	blast.	5 "	2,604	30	no living flies
100	pre-bl.	15 "	2,604	38	living flies
100	blast.	15 "	2,604	15	no living flies
100	pre-bl.	7.5 "	1,543	53	living flies
100	blast.	7.5 "	1,543	27	no living flies
100	pre-bl.	22.5 "	1,543	29	living flies
100	blast.	22.5 "	1,543	20	no living flies

Of these, however, some in each case showed somatic deformities: 24 out of the total 176 living flies, or a percentage of 13.6363 ± 1.74466. The malformations produced consisted of twisted head or thorax, varying degrees of the absence of wings with the remnants crumpled and torn, and in one case absence of legs on one side of the body. This one individual, a male, was non-viable and died two days after emergence. All others gave normal viable offspring, there being no indication in three generations that the defects were heritable. No sterility in the adult fly was brought about by exposure to alpha-radiation. The deformities produced recall those reported by Lacassagne and Desclin (1928) in studies of the effects of alpha-radiation upon the eggs and young embryos of frogs.

Thus the results of exposure to the alpha-rays of radium F differ considerably from those brought about by beta or gamma radiation. This is a brief preliminary report; the experiments are being continued and extended.

The authors find pleasure in expressing their appreciation to members of the staff of the Curie Foundation Institute for the opportunity to carry on the investigations reported here.

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THE INHERITANCE OF DICHROMATISM IN THE DEER-MOUSE, *PEROMYSCUS MANICULATUS BLANDUS*[1]

THE occurrence of two or more color phases in one species at the same geographical locality has been described for a number of kinds of mammals. A well-known example is the gray squirrel of eastern North America, which in many localities has both gray and black phases.

In the mice of the genus Peromyscus, Osgood[2] has described the occurrence of two color phases in *Peromyscus maniculatus gambelii,* in *P. m. blandus,* in *P. m. sonoriensis* and in *P. m. coolidgei.* In none of these races are the two color phases sharply alternative, for in each race some specimens are intermediate in color tone.

The buff and the gray color phases of *Peromyscus m. gambelii* from southwestern California were each found by Collins[3] to breed true, but when these extremes were hybridized, the offspring were intermediate in color, and the mice of the F_2 generation likewise were intermediate between the two color phases.

Peromyscus maniculatus blandus is said by Osgood to have a buff color phase, which is similar to the color of *sonoriensis,* and a gray phase, which is unique. "All stages of variation between the two phases occur." Both of these color phases occur at Alamogordo, New Mexico, where 56 mice of this subspecies were collected by the University of Michigan-Walker-Harris Expedition of 1927.[4] Some of these animals were brought to Ann Arbor alive and became the parents of an extensive stock; others were put up in the field as round or flat skins. Of the total

[1] The completion of this study was made possible by a research grant from the American Association for the Advancement of Science.

[2] W. H. Osgood, *U. S. Dept. Agric., North Amer. Fauna,* No. 28, 1909.

[3] H. H. Collins, *Jour. Exp. Zool.,* 38: 91–92, 1923.

[4] L. R. Dice, *Univ. Mich., Occ. Papers Mus. Zool.,* No. 213, p. 25, 1930.

number of field-caught mice prepared as specimens, 9 are too immature for certain determination of their color phase, 16 are certainly buff, 20 are gray, and 11 are more or less intermediate between buff and gray. Osgood's statement that all intermediate stages of color occur is true, for no sharp line between buff and gray can be drawn in this series.

Among the breeding stock of *blandus* brought to the University of Michigan, two females were buff, while all the other animals were gray. By mating these buff females to gray males some buff offspring were secured. Matings of gray with gray produced gray offspring, and therefore the possibility was suggested that gray was recessive to buff. Extensive further matings have tended to confirm this hypothesis.

From matings of gray × gray I have records of 41 gray females and 42 gray males, and also 1 buff male. This buff individual was not saved as a specimen, and possibly was wrongly identified. From matings of buff × buff I have records of 3 buff females and 2 buff males. Evidently the sex ratios are about equal in both the gray and the buff phases.

From matings of gray × buff (heterozygous for gray) were obtained 73 gray, 76 buff, and two intermediate (expected 75.5 gray : 75.5 buff). From gray × buff (possibly heterozygous for gray) were secured 30 gray and 31 buff (expected 30.5 : 30.5). From matings of gray × buff (probably homozygous) were obtained 14 buff (expected 14 buff). These results indicate that gray is recessive to buff and that the two colors are allelomorphs, behaving in inheritance as a simple mendelian character difference. There is, however, a discrepancy due to the occurrence of a few intermediates. These perhaps may be due to modifying factors, which mask the clear expression of the color phases.

Intermediates are not so numerous among the laboratory-bred mice as in those collected in the field. This may partly be owing to the fact that the laboratory-bred animals are of known age and therefore are certainly fully mature, while some of the wild-killed animals are obviously immature. I have found that color phase determinations are often erroneous if made before the mice are six months of age.

Another possible reason for fewer intermediates in the laboratory-bred stock is that the laboratory parents were selected both for buff and for gray, and those of intermediate character were

not used for breeding. If, as is probable, the *blandus* stock contained various color modifiers, these would tend to be eliminated by the selection, leaving buff and gray to show in a less obscured manner.

A color modifier of proved potency has actually been found in the stock. This is a dilution factor affecting both the gray and the buff phases. Its principal effect is greatly to reduce the amount of black on the tips of the hairs, so that the animals appear much paler. With the amount of black in the pelage reduced, the difference between the gray and buff color phases is much more apparent.

The dilute character was first noted in several offspring from a female, the daughter of two field-caught mice, mated with her son, who was fathered by her brother. There was therefore much inbreeding in this strain, and it is probable that the dilution factor was present in the original wild stock.

The dilution factor seems definitely inherited, and while its genetics have not been worked out, it seems to behave as a single-unit Mendelian recessive to full color. From matings of dilute × dilute 18 offspring are dilute, as would be expected under this hypothesis.

Another color modification which has arisen in the *blandus* stock is a white spot on the crown of the head. Similar white spots on the head have been found in many different subspecies of *Peromyscus maniculatus* and *P. leucopus,* sometimes in specimens taken in the field. However, I have not found such white head spots in wild *blandus.* The white spot arising in the laboratory-bred *blandus* is definitely inherited. From parents both of which had white spots on the crown 8 young all had varying amounts of white on this part of the head.

The white spots occurring on the head in other races of Peromyscus are also inherited, though in a variable manner. Sometimes the occurrence of a white tip to the tail seems to be correlated with the occurrence of the white spot on the head. By selection it seems possible to increase the size of these white spots to some extent. Sumner[5] also has noted the occurrence of white spots on the head in "various races of Peromyscus," and Castle[6] states that "The production of white-spotted races from small

[5] F. B. Sumner, *Bibliographia Genetica,* 9: 38, 1932.

[6] W. E. Castle, "Genetics and Eugenics," ed. 2, p. 125, 1920.

beginnings observed in wild stocks has been accomplished in the laboratory by Castle and Phillips in the case of Peromyscus."

While the occurrence of the character for white spotting in wild deer-mice probably does not ordinarily affect the color of much of the animal, yet it is very likely that numerous other hereditary color variations occur, and some of these, like the dilution factor, probably do affect the expression of the color phases. It seems justifiable, therefore, to assume that some unknown color modifiers cause the production of the apparent intermediates between the color phases.

A great deal of variability in hereditary factors undoubtedly occurs in all wild populations of Peromyscus. In another paper[7] I have demonstrated that in a population of *Peromyscus m. rufinus* taken in Colorado, there is a large amount of genetic variability in size factors and some variability in color factors. The dichromatism of *blandus* is another illustration of the extent of genetic variability in the wild populations of these deer-mice.

SUMMARY

The extremes of the gray and buff color phases of the deer-mouse, *Peromyscus maniculatus blandus,* behave in heredity as Mendelian allelomorphs, gray being recessive to buff. However, among the experimental animals several can not be assigned with certainty to either color phase, and in the series of specimens of wild animals there is an appearance of complete intergradation between the two color phases.

Several inherited factors modifying color and pattern are shown to occur in the subspecies, and it is assumed that other unknown modifying factors mask in some individuals the clear expression of the color phases, and thus produce the apparent intermediates.

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[7] L. R. Dice, *Univ. Mich., Occ. Papers Mus. Zool.,* No. 271, in press.

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